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Announcement/Avis

Journal Title to Change January 1980

Effective with the January 1980 issue, the name of the ***Journal*** will be changed to the ***Canadian Journal of Fisheries and Aquatic Sciences.*** Numbering of the Journal will begin at Volume 37, Number 1. This change resulted from a Canadian Government Bill which repealed the Fisheries Research Board Act.

The title of the other series of our publications will be changed as follows:

— *Bulletin of the Fisheries Research Board of Canada* to ***Canadian Bulletin of Fisheries and Aquatic Sciences.***

— *Miscellaneous Special Publication* to ***Canadian Special Publication of Fisheries and Aquatic Sciences.***

— *Technical Report* to ***Canadian Technical Report of Fisheries and Aquatic Sciences.***

— *Manuscript Report* to ***Canadian Manuscript Report of Fisheries and Aquatic Sciences.***

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— *Data Report* to ***Canadian Data Report of Fisheries and Aquatic Sciences.***

— *Translation series* to ***Canadian Translations of Fisheries and Aquatic Sciences.***

Modification de titre du *Journal* en janvier 1980

À compter du numéro de janvier 1980, soit le n° 1, volume 37, le titre du *Journal* deviendra le ***Journal canadien des sciences halieutiques et aquatiques.*** Cette modification fait suite à la présentation d'un projet de loi du gouvernement canadien qui a annulé la Loi sur le Conseil des recherches sur les pêcheries.

Les titres des autres publications seront aussi modifiés comme suit:

— Le *Bulletin de l'Office des recherches sur les pêcheries du Canada* devient ***Bulletin canadien des sciences halieutiques et aquatiques.***

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— Le *Rapport à l'industrie* devient ***Rapport canadien a l'industrie sur les sciences halieutiques et aquatiques.***

— Le *Rapport statistique* devient ***Rapport statistique canadien des sciences halieutiques et aquatiques.***

— La *série de traductions* devient ***Traductions canadiennes en sciences halieutiques et aquatiques.***

Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 36, No. 10, October 1979

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Changes in the Apparent Temperature Optima of the Plankton of Lake Michigan at Chicago, Illinois

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MAKAREWICZ, J. C., R. I. BAYBUTT, AND K. DAMANN. 1979. Changes in the apparent temperature optima of the plankton of Lake Michigan at Chicago, Illinois. J. Fish. Res. Board Can. 36: 1169–1173.

Forty years (1937–76) of data from Lake Michigan water intakes at Chicago, Illinois, were examined to explain reported differences in the apparent temperature optima of phytoplankton. The bimodal seasonal plankton distribution, typical at Chicago, still occurs. However, there has been a shift in seasonal periodicity with spring peaks occurring in March from 1957 to 1976 instead of May–June as previously reported for 1937–56. An optimum temperature of 10°C for the plankton community was observed between 1936 and 1956, while for the last 20 yr an optimum temperature range from 0 to 4°C was observed. This change in optimum temperature of the plankton community is related to a change in the abundance of the genera *Asterionella*, *Fragilaria*, *Stephanodiscus*, and *Tabellaria*. *Asterionella* and *Fragilaria* were the dominant spring plankton with maximum standing crops observed around 10°C prior to 1956. *Stephanodiscus* first increased significantly in 1957 and was the dominant spring plankter through 1976. More recently (1972–76), blue-green algae have increased in numbers. Differences in apparent temperature optima reported are real and are caused by the emergence of cold water species of *Stephanodiscus* as the dominant spring plankter from 1957 to 1976.

Key words: plankton, temperature optima, Lake Michigan

MAKAREWICZ, J. C., R. I. BAYBUTT, AND K. DAMANN. 1979. Changes in the apparent temperature optima of the plankton of Lake Michigan at Chicago, Illinois. J. Fish. Res. Board Can. 36: 1169–1173.

Nous avons analysé les températures observées sur une période de quarante ans (1937–76) à des prises d'eau du lac Michigan à Chicago, Illinois, afin d'expliquer les différences signalées dans la température optimale apparente du phytoplancton. Il se produit encore une distribution saisonnière bimodale du plancton, typique à Chicago. Mais il y a eu glissement de périodicité saisonnière, les pics printanniers survenant en mars, de 1957 à 1976, au lieu de mai–juin durant les années 1937 à 1956. Entre 1936 et 1956, on observe une température optimale de 10°C pour la communauté planctonique, alors que durant les 20 dernières années on observe une température optimale entre 0 et 4°C. Ce changement dans la température optimale de la communauté planctonique est lié à un changement dans l'abondance des genres *Asterionella*, *Fragilaria*, *Stephanodiscus* et *Tabellaria*. Avant 1956, *Asterionella* et *Fragilaria* étaient les

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espèces printannières dominantes, avec biomasses maximales observées autour de 10°C. *Stephanodiscus* commença à augmenter appréciablement en 1957 et fut le planctonte printannier dominant jusqu'en 1976. Récemment (1972–76), les algues vertes sont devenues plus abondantes. Ces différences de température optimale sont réelle et sont dues à l'apparition d'espèces d'eau froide du genre *Stephanodiscus* comme planctontes printanniers dominants de 1957 à 1976.

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A diverse literature exists on the phytoplankton of Lake Michigan (Tarapchak and Stoermer 1976). However, with the exception of Damann's analyses (1945, 1960, 1966) and those of Stoermer and Yang (1970), no long-term studies on Lake Michigan phytoplankton are available. Over a 23-yr period (1940–63), Damann (1966) observed a bimodal seasonal curve for plankton in the nearshore region near Chicago and that a temperature of 10°C coincided with the occurrences of spring and fall peaks of total plankton. He suggested that 10°C was the optimum temperature for plankton development in Lake Michigan. Based on samples collected at nearshore and offshore stations in southern Lake Michigan from April through October 1971, Stoermer and Ladewski (1976) observed that no species developed a maximum between 9 and 13°C. We investigated the apparent discrepancies between these two workers' results.

Materials and Methods

Temperature optima for total plankton from 1937 to 1976 were examined to determine changes in the bimodal seasonal pattern and to document changes in species abundance. Phytoplankton data (1937–76) from the central and south cribs of the Chicago Water Filtration Plant were used in the analysis of Lake Michigan plankton data. Both cribs are located approximately 3.5 km offshore in 10 m of water with the intakes at a depth of approximately 7.0 m. The south crib is located 15.7 km south of the central crib. Plankton were counted by the Sedgewick–Rafter method (APHA et al. 1960). Further details on sample collection and phytoplankton counting procedures at the Chicago Water Filtration Plant are given in Damann (1945, 1960).

We define apparent optimum temperature as the temperature of maximum population density of the total plankton or individual genera with all other parameters at their optimum naturally realizable value, following Stoermer and Ladewski (1976). Phytoplankton data were summarized for 5-yr periods using multiple and linear regression techniques. Up to 1967, optimum temperatures were calculated from polynomial regressions modeled on the general formula of a parabola ($Y = ax^2 + bx + c$), where X = temperature in °C, and Y = total plankton in cells/mL (Fig. 1b). Data from 1967 to 1976 did not show significant (F ratio is not significant at $P = 0.01$) curvilinear patterns of total plankton on temperature. During these years, linear regression analysis was employed to predict temperature optima (Fig. 1a).

Results

Diatoms have been the dominant plankton group in

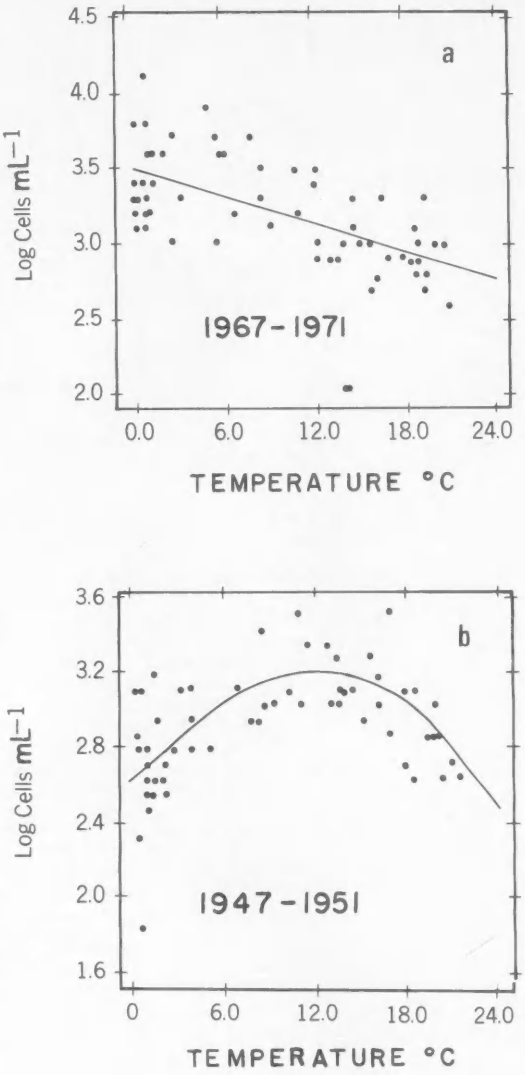

FIG. 1. Average monthly plankton density versus average monthly temperature. Data from the Central and South Cribs have been averaged. In a, $Y = 3.489 - 0.0297t$. In b, $Y = 2.664 + 0.0968t - 0.0043t^2$ where t = temperature.

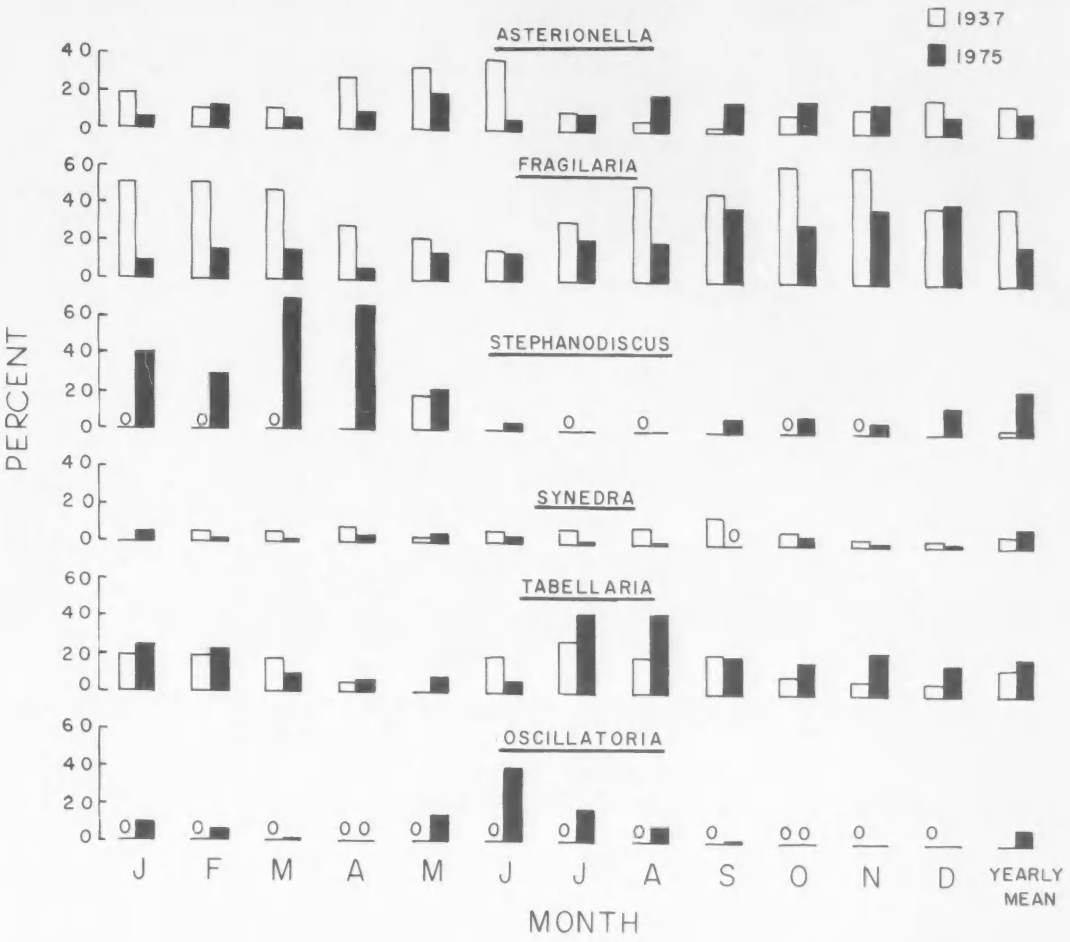

FIG. 2. Comparison of monthly plankton densities of selected genera (1937 vs. 1975) in Lake Michigan at Chicago. Values are expressed as percent of total standing crop of the Central Crib. 0 = cell counts below detection limit of counting method.

TABLE 1. Optimum temperature (°C) of the phytoplankton community (South Crib) in Lake Michigan at Chicago. Optimum temperatures were calculated by three methods: (1) regression analysis; (2) regression analysis with a $\log_{10}$ transformation of the plankton counts; and (3) the average monthly temperature at the occurrence of the maximum spring standing crop.

Years	Optimum temperature (°C)		Average temperature (°C) of maximum crop
	Plankton counts	Log plankton counts	
1937–41	10.9	11.5	13.8
1942–46	10.4	10.7	9.6
1947–51	10.9	11.2	10.8
1952–56	10.1	10.3	14.0
1957–61	3.1	4.6	1.0
1962–66	1.0	3.3	1.0
1967–71	0.0	0.0	0.0
1972–76	0.0	0.0	2.5

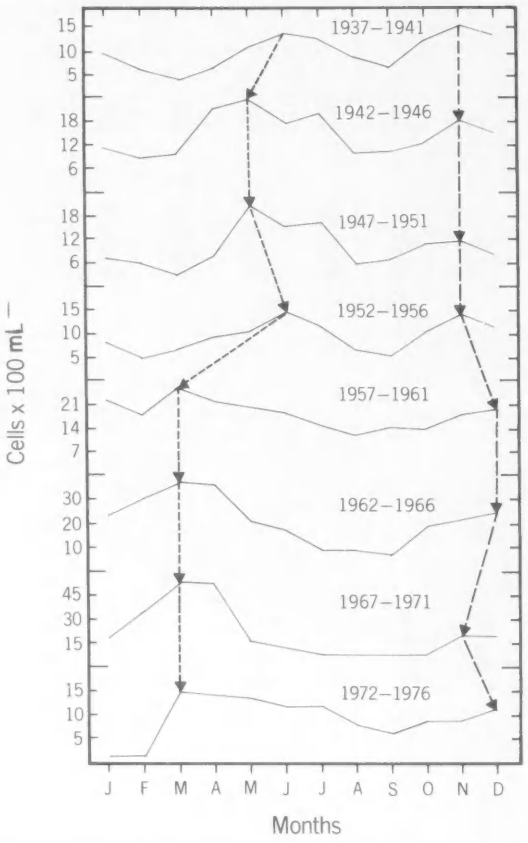

FIG. 3. Mean monthly plankton standing crops (South and Central Cribs) for 5-yr intervals (1937–76) in Lake Michigan at Chicago.

the nearshore region at Chicago over the past 40 yr. A monthly comparison of the years 1937 and 1975 illustrates the general changes that occurred in the plankton community near Chicago (Fig. 2). From 1937 to 1956 *Asterionella*, *Fragilaria*, *Synedra*, and *Tabellaria* were the dominant genera near Chicago, accounting for 84.1% of the total standing crop. During this 20-yr period, the relative abundance of *Stephanodiscus* was less than 1% of the total plankton community. After 1956 *Stephanodiscus* became more abundant, accounting for 20% of the total standing crop from 1956 to 1977, and it reached a maximum of 82% of the plankton community in February 1961. Between 1972 and 1977, *Stephanodiscus* decreased in abundance while blue-green algal species of the genus *Oscillatoria* increased to 6% of the plankton community in 1975 (37% of the total standing crop for the month of June 1975) (Baybutt and Makarewicz 1979).

Examination of the bimodal seasonal distribution

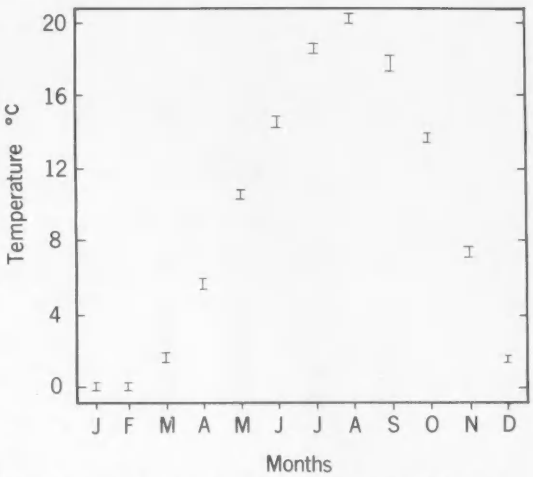

FIG. 4. Mean ± SE monthly temperatures (°C) of Lake Michigan at Chicago (1937–76).

curve of plankton at 5-yr intervals indicated a definite displacement in the timing of plankton maxima with spring peaks shifting from May–June (1937–56) to March (1957–76) (Fig. 3). From 1937 to 1956 the maximum density of total plankton occurred from 10 to 11.5°C. Between the years 1957 and 1976, a substantial reduction in temperature optima was observed. Analyses show that a reduction from approximately 10°C, as noted in the past, to 0–4°C occurred (Table 1). From 1936 to 1976 seasonal water temperatures of Lake Michigan at Chicago have not altered significantly (Fig. 4).

Discussion

The differences in temperature optima reported by Stoermer and Ladewski (1976) and Damann (1966) are due in part to differences in approach. Stoermer and Ladewski calculated temperature optima for *individual* species during a 7-mo period (April–October) of 1971 and reported no species with optima between 9 and 13°C. Damann calculated temperature optima for the plankton community for several consecutive years and found a community temperature optimum of 10°C for 1928 to 1963. A period of 8 yr separates the ending and beginning of each study.

Damann's value of 10°C was the result of averaging high and low temperature optima of various genera and species. Closer examination indicates four genera accounted for 85.8% of the community in 1937. Two genera, *Asterionella* and *Fragilaria*, constituted 59.7% of the standing crop and attained maximum densities at 8.9 and 12.0°C, respectively. Blooms of these two genera coincided with the spring and fall pulses. When grouped together with other species, a temperature optimum for the total plankton community of approximately 10°C resulted.

Analyses from 1967 to 1976, however, indicated a temperature optimum of 0 to 2.5°C for the phytoplankton community of Lake Michigan (Table 1). *Stephanodiscus binderanus* (Kützing) Krieger and *S. tenuis* Hustedt were rare prior to 1956 in the Chicago area. Between 1956 and 1976 these two species were dominant, accounting for 20% of the total annual standing crop. More interestingly, their abundance peaked in the early spring with values as high as 70–80% of the plankton community. *Stephanodiscus binderanus* and *S. tenuis* attained their maximum standing crop in the spring at temperatures between 0 and 4°C, an optimum temperature range significantly different from Stoermer and Ladewski's (1976) reported 6.3–8.9°C for the same two species. However, our data indicate that the maximum spring peak for these two species occurs in March at Chicago during the period 1956–76, a month earlier than when Stoermer and Ladewski began their 7-mo investigation of phytoplankton at inshore and offshore stations. Our analysis on genera other than *Stephanodiscus* reveal an apparent optimum temperature similar to those reported by Stoermer and Ladewski (1976).

What is evident from our study of community temperature optima over a 40-yr period (1926–76) is that a significant change has occurred in the apparent optimum temperature of the plankton community of Lake Michigan and that a shift has occurred in the bimodal curve of seasonal distribution with the spring pulse occurring earlier in the year. These changes are undoubtedly related to the emergence of *Stephanodiscus* as the dominant spring plankter within Lake Michigan near Chicago. Because the seasonal temperatures of Lake Michigan have not altered significantly through 40 yr (Fig. 4), it is apparent that the influence of other environmental factors have affected species composition and abundance, notably the accelerated cultural eutrophication of Lake Michigan.

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Obligate Anaerobic Bacteria in the Gastrointestinal Microflora of the Grass Carp (*Ctenopharyngodon idella*), Goldfish (*Carassius auratus*), and Rainbow Trout (*Salmo gairdneri*)

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TRUST, T. J., L. M. BULL, B. R. CURRIE, AND J. T. BUCKLEY. 1979. Obligate anaerobic bacteria in the gastrointestinal microflora of the grass carp (*Ctenopharyngodon idella*), goldfish (*Carassius auratus*), and rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 1174–1179.

Grass carp (*Ctenopharyngodon idella*), bred in Arkansas and maintained in British Columbia under defined culture conditions on pelleted diets and on aquatic weeds, were examined to determine their commensal gastrointestinal bacterial flora. Using anaerobic incubation, the total bacterial numbers cultured ranged from 6×10^4 to 4×10^8 (average 4×10^6) per g of alimentary tract plus contents. Obligately anaerobic bacteria were isolated and identified as species of *Actinomyces*, *Bacteroides*, *Eubacterium*, *Fusobacterium*, and *Peptostreptococcus*. This is the first description of the presence of these strictly anaerobic organisms in the gastrointestinal tract of fish. Indeed, many of the anaerobes isolated did not conform to previously described species. Members of the Genus *Clostridium* were also isolated by enrichment culture and appeared to be associated with a pond weed diet. A wide variety of facultative anaerobic bacteria were also isolated, with *Aeromonas hydrophila* predominating. The gastrointestinal tracts of goldfish (*Carassius auratus*) were also found to contain sizable numbers of obligate anaerobes, but the gastrointestinal tracts of hatchery-cultured rainbow trout (*Salmo gairdneri*) contained insignificant numbers.

Key words: grass carp, anaerobic bacteria, gastrointestinal microflora, *Aeromonas hydrophila*, rainbow trout, goldfish

TRUST, T. J., L. M. BULL, B. R. CURRIE, AND J. T. BUCKLEY. 1979. Obligate anaerobic bacteria in the gastrointestinal microflora of the grass carp (*Ctenopharyngodon idella*), goldfish (*Carassius auratus*), and rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 1174–1179.

Nous avons examiné des carpes d'herbe (*Ctenopharyngodon idella*), produites en Arkansas et élevées en Colombie-Britannique dans des conditions définies avec régimes alimentaires de boulettes et d'herbes aquatiques, dans le but de déterminer leur flore bactérienne gastro-intestinale commensale. Dans une incubation anaérobie, le nombre total de bactéries cultivées varie de 6×10^4 à 4×10^8 (moyenne de 4×10^6) par g de tractus digestif plus contenus. Nous avons isolé les bactéries obligatoirement anaérobies et les avons identifiées comme espèces d'*Actinomyces*, *Bacteroides*, *Eubacterium*, *Fusobacterium* et *Peptostreptococcus*. C'est la première fois qu'est signalée la présence de ces organismes strictement anaérobies dans le tractus gastro-intestinal des poissons. En fait, plusieurs des anaérobies isolés ne ressemblent pas à des espèces déjà décrites. Une culture avec enrichissement nous a permis d'isoler des membres du genre *Clostridium* qui semblent associés à un régime alimentaire d'herbe à brochets. Nous avons également isolé une grande variété de bactéries anaérobies facultatives, avec prédominance d'Aeromonas hydrophila. On a en outre découvert que le tractus gastro-intestinal des carassins (*Carassius auratus*) contenait des quantités appréciables d'anaérobies obligatoires, mais que celui de truites arc-en-ciel (*Salmo gairdneri*) de pisciculture en contenait des quantités négligeables.

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THE gastrointestinal tract of homeothermic animals is populated by large numbers of a wide variety of bacteria (Smith and Crabb 1961; Drasar and Hill 1974; Mushin and Ashburner 1964). Although faculative anaerobes are present in this microflora, the predominant species are strict anaerobes (Drasar and Hill 1974) and in the colon these obligate anaerobes outnumber the facultative species by at least 1000 to 1 (Finegold et al. 1977). The gastrointestinal tract of fish appears to have a simpler microflora than that of homeotherms and the predominant bacteria isolated from the fish gut have been aerobes or facultative anaerobes (Trust and Sparrow 1974; Horsley 1977). Although spore forming anaerobes have also been isolated in small numbers (Shewan 1961), these clostridia

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were regarded as food-borne transients, and other investigations of the gut microflora of hatchery trout failed to demonstrate the presence of the obligately anaerobic Gram-negative bacteria which are present in such large numbers in homeotherms (Trust 1975; Trust et al. 1978). Indeed, the only reports of the isolation of non-spore forming anaerobes associated with fish are by Henley and Lewis (1976) and Udey et al. (1977) who described the pathogen *Eubacterium tarantellus* in marine species. Neither group reported a gastrointestinal origin for this bacterium.

This is the first report of the presence of obligate anaerobes among the resident bacterial flora of grass carp, goldfish and rainbow trout.

Materials and Methods

Fish

Juvenile grass carp (*Ctenopharyngodon idella*) were purchased from Leon Hill's Catfish Hatchery, Lonoke, Arkansas. The fish were shipped to Victoria in oxygenated plastic bags and were in transit for approximately 36 h. All fish were in reasonable condition on arrival and were transferred to glass or enamelled tanks containing well water at 22°C. Glass aquaria were equipped with individual external filters, while water in the enamelled tanks was recycled through an external filtering unit. Partial renewal of the tank water and cleaning of the filtering units was undertaken as required to maintain total ammonia nitrogen, nitrates and nitrites within acceptable ranges. All tanks were supplied with airstones and dissolved oxygen was maintained above 6 mg/L; pH varied in the range of 7–8. The density of fish in each tank never exceeded 5 g/L of water. Fish were fed Purina catfish chow or pelleted diets formulated at the University of Victoria for 6 wk prior to sampling. The grass carp ranged in weight from 2.8 to 247.5 g; the average weight of the fish examined was 32 g. Rainbow trout (*Salmo gairdneri*) (average weight 40 g) were taken from the population maintained at this laboratory under the conditions previously described (Trust 1975; Trust et al. 1978). Goldfish (*Carassius auratus*) (average weight 32 g) were purchased from a local retail outlet.

Bacteriological Sampling

Fish were netted, killed by a blow to the head, and the entire gastrointestinal tract removed by aseptic surgery. Dissections were performed in the anaerobic environment after preliminary experiments indicated that the procedure yielded a better recovery of anaerobes. All subsequent procedures were performed anaerobically. The gastrointestinal tract was then weighed, placed in a sterile plastic bag, and a suitable amount of diluent was added to effect a tenfold dilution. The diluent used was that recommended by Holdeman et al. (1977). The sample was then placed in a Colworth Stomacher (A. J. Seward Ltd., Bury St., Edmunds, Suffolk, England) and homogenized for 30 s to 1 min.

The resulting homogenized sample was serially diluted and plated onto a variety of media which were incubated aerobically or anaerobically at 37°C. The plating media included trypticase soy agar [TSA] (Baltimore Biological Laboratories), brain heart infusion agar [BHIA] (BBL), reinforced *Clostridium* medium [RCM] (BBL), peptone yeast extract glucose agar [PYGA], McClung-Toabe egg yolk agar (modified) [EYA], peptone yeast extract serum cocarboxylase [PYSC], and *Brucella* blood agar [BBA] (Holdeman et al. 1977).

Anaerobiosis in the McCoy anaerobic cabinet was obtained with a 10% H_2:5% CO_2:85% N_2 gas mixture. Preliminary experiments revealed that recovery of anaerobes was enhanced by the incorporation of CO_2 in the chamber atmosphere. On occasions BBL anaerobic jars and GasPak anaerobic envelopes were also employed.

Identification of Bacteria

Strictly anaerobic bacteria were isolated from a plate which contained countable numbers of colonies. A representative of each colony type was plated on peptone yeast extract glucose agar (PYGA), *Brucella* blood agar (BBA) or brain heart infusion agar (BHIA), and purified by a second streaking onto the same medium. In an attempt to isolate nutritionally fastidious anaerobes similar to those associated with ruminants, samples were also enriched in E broth (Holdeman et al. 1977) and thioglycollate broth (BBL) and streaked onto PYGA after incubation for 3 to 5 d. Clostridia were isolated selectively by the procedure of Koransky et al. (1978). After purification, isolates were maintained in cooked meat glucose medium (CMG, 1% w/v glucose) at room temperature. All media used in the growth of anaerobes were prepared according to the formulations of Holdeman et al. (1977), except that cooling of the media was allowed to proceed in the anaerobic conditions afforded in the airlock of the anaerobic chamber.

The purified anaerobes were identified on the basis of their Gram reactions using the Kopeloff modification (Holdeman et al. 1977), their gas liquid chromatographic profiles and their biochemical properties using the biochemical tests of the Minitek System (BBL). Cultures grown in PYGA or CMG at 20° for 5 d were analyzed for volatile fatty acids or for methyl derivatives of pyruvic, lactic, fumaric, and succinic acids by the procedures recommended by Holdeman et al. (1977). Samples were analyzed by a Varian model 3700 GLC with flame ionization detector using a temperature program starting at 125°C, increasing at 10°C per min to a final temprature of 195°C. The fatty acids were separated on a $\frac{1}{8}'' \times 6'$ stainless steel column of 10% SP-1200, 1% H_3PO_4 on Chromasorb WAW (Supelco). Anabac standards (Capco, Sunnydale, California) and uninoculated PYGA or CMG were included as reference standards and as controls. Sample sizes varied from 0.5 to 3.0 μL.

The biochemical properties examined included fermentation of arabinose, mannitol, salicin, sucrose, glucose, glycerol, xylose, lactose, and maltose, hydrolysis of esculin, production of indole, and reduction of nitrate. Other tests which were performed on some strains were gas production in PYG agar deep culture, curd and digestion in milk, conversion of threonine to propionate, and acid production after growth in glucose or starch. Identification of isolates was based on the schemes of Holdeman et al. (1977), Buchanan and Gibbons (1974), and the scheme accompanying the Minitek System.

Facultative anaerobic bacteria were isolated and identified as previously described (Trust and Sparrow 1974; Trust 1975). The API strip method (Analytab Products, Inc.) was used to confirm the identity of many of the isolates and some identities were established in conjunction with the API computerized profile index. The ability of isolates to utilize cellulose, carboxymethyl–cellulose, and cellobiose was tested, as was the ability to degrade starch.

TABLE 1. Numbers of bacteria present in the gastrointestinal tract of grass carp, goldfish, and rainbow trout.

	Incubation conditions	No. of estimates	Number of viable bacteria/g of gastrointestinal tract plus contents	
			Average	Range
		Grass carp		
Total tract	Anaerobic			
	TSA[a]	6	6.5×10^7	(3.2–23.0)
	BHIA[b]	5	4.8×10^7	(0.4–16.6)
	RCM[c]	2	6.6×10^4	(5.9–7.3)
	PYGA[d]	4	7.7×10^7	(0.1–22.4)
	EYA[e]	3	4.2×10^7	(0.1–7.6)
	PYSC[f]	2	2.5×10^7	(0.1–4.9)
	BBA[g]	12	9.3×10^7	(0.1–46.0)
	Aerobic			
	TSA	26	9.6×10^7	(0.4–34.0)
Foregut[h]	Anaerobic			
	BBA	3	5.0×10^6	(1.0–10.0)
	BHIA	3	1.2×10^7	(1.0–1.4)
	PYGA	3	1.0×10^7	(0.6–1.6)
	Aerobic			
	TSA	3	4.0×10^6	(1.6–7.1)
Midgut[h]	Anaerobic			
	BBA	3	3.3×10^7	(0.1–9.2)
	BHIA	3	3.6×10^7	(2.5–6.7)
	PYGA	3	6.0×10^7	(2.2–12.0)
	Aerobic			
	TSA	3	1.8×10^7	(1.0–3.1)
Hindgut[h]	Anaerobic			
	BBA	3	3.3×10^8	(1.0–5.8)
	BHIA	3	1.6×10^9	(0.3–2.1)
	PYGA	3	3.7×10^8	(1.8–6.3)
	Aerobic			
	TSA	3	4.4×10^7	(1.3–6.1)
		Goldfish		
Total tract	Anaerobic			
	BBA	2	3.8×10^8	—
	BHIA	2	4.0×10^8	—
	PYGA	2	1.6×10^8	—
	Aerobic			
	TSA	2	1.8×10^8	—
		Rainbow trout		
Total tract	Anaerobic			
	BBA	2	TFTC[i]	—
	BHIA	2	TFTC	—
	PYGA	2	TFTC	—
	Aerobic			
	TSA	2	1.8×10^2	—

[a]TSA is trypticase soy agar; [b]BHIA is brain heart infusion agar; [c]RCM is reinforced *Clostridium* medium; [d]PYGA is peptone yeast extract glucose agar; [e]EYA is McClung–Toabe egg yolk agar; [f]PYSC is peptone yeast extract serum cocarboxylase agar; [g]BBA is *Brucellla* blood agar; [h]Values are the results obtained from 3 estimates each with 5 fish; [i]TFTC is too few organisms to count.

The ability to degrade cellulose was tested in 2% (w/v) bacto–cellulose (Difco) mineral salts agar, filter paper–mineral salts broth, and 2% (w/v) carboxymethyl–cellulose (Pharmacia) mineral salts agar. On occasions 0.5% (w/v) glucose was added to the various cellulose media in an attempt to stimulate cellulose degradation (Skerman 1969). Cellobiose activity was tested in 1% (w/v) cellobiose–phenol red nutrient agar, and amylase activity employed 2% (w/v) starch nutrient agar. Proteolytic activity was tested in 2% (w/v) skim milk agar and in proteolytic agar, while lipolytic activity was tested in 2% (w/v) tributyrin agar.

TABLE 2. Strictly anaerobic bacteria isolated from the gastrointestinal tract of grass carp, goldfish, and rainbow trout.

Organism	No. of isolations	No. of samples from which isolated
Grass carp[a]		
Actinomyces	1	1
Bacteroides	39	13
Clostridium[b]	57	5
Eubacterium	24	7
Fusobacterium	32	10
Peptostreptococcus	4	3
Unidentified	98	12
Goldfish[c]		
Bacteroides melaninogenicus	5	2
Bacteroides thetaiotaomicron	2	2
Bacteroides sp.	4	2
Unidentified	1	1
Rainbow trout[c]		
Bacteroides melaninogenicus	1	1
Clostridium[b]	3	2
Fusobacterium	15	2
Unidentified	6	2

[a]A total of 20 fish was examined.
[b]Isolated by enrichment culture.
[c]A total of two fish was examined.

TABLE 3. Other microorganisms isolated from the gastrointestinal tract of grass carp.

Organism	No. of isolates	No. of samples from which isolated
Acinetobacter	21	8
Aeromonas hydrophila	292	36
Alcaligenes	5	4
Bacillus	9	8
Citrobacter	26	16
Enterobacter	1	1
Escherichia	3	3
Flavobacterium	12	7
Micrococcus	7	4
Moraxella	4	3
Pasteurella	15	7
Proteus	3	1
Pseudomonas	150	37
Salmonella arizonae	1	1
Streptococcus	14	3
Vibrio	33	6
Yersinia enterocolitica	96	29

[a]Total number of fish examined was 37.

Results

The results in Table 1 show the numbers of viable bacteria recovered when the gastrointestinal tract and its contents were sampled. With the exception of RCM, which was selective and yielded only 10^4 bacteria/g, anaerobic incubation on the various media generally allowed the recovery of from 2.5 to 9.3×10^7 colony forming units per gram in grass carp. Similar numbers of bacteria were recovered under aerobic or anaerobic incubation of the plates. Quantitative differences in bacterial numbers were not seen in grass carp on pelleted or weed diets. However, distribution of bacteria along the length of the tract shows that the hindgut was most heavily colonized. Bacterial counts obtained in the goldfish were even higher than those obtained in the grass carp, both aerobically and anaerobically. In these fish, the numbers of bacteria recovered were higher with anaerobic incubation of the plates. The bacterial numbers in the gastrointestinal tract of trout were a great deal lower than in the grass carp or goldfish. As in previous studies, very few aerobes were present in the trout gastrointestinal tract under the fish culture conditions employed. On anaerobic incubation, too few bacteria could be cultured to meaningfully record the count.

Many of the organisms present on the anaerobic plates from grass carp were strict anaerobes. Species of *Eubacterium*, *Fusobacterium*, and *Bacteroides* were predominant while clostridia were present in such low numbers that enrichment culture was required for their isolation (Table 2). Incorporation of 0.1% (w/v) Fe_2SO_4 in BBA facilitated the selective isolation of *Bacteroides melaninogenicus* since many of these colonies turned black after 5 d incubation. Among the other species of *Bacteroides* examined, *Bacteroides fragilis*, *Bacteroides ovatus*, *Bacteroides thetaiotaomicron*, *Bacteroides vulgatus*, and *Bacteroides distasonis* were all characterized, as were *Fusobacterium mortiferum*, *Fusobacterium nucleatum*, *Fusobacterium varium*, and *Fusobacterium necrophorum*. Many of the strict anaerobes isolated are previously undescribed, and their identity will be the subject of another report. Gram-positive cocci were present among these unidentified species, but the majority were Gram-negative rods. Enrichment in the rumen fluid containing E broth did not allow the isolation of the more fastidious species commonly isolated from herbivores.

A variety of facultative anaerobes and aerobes were also isolated from grass carp. Table 3 shows that the predominant species recovered was *Aeromonas hydrophila*. This facultative anaerobe was present in almost all of the samples and comprised 42% of these isolates. Pseudomonads were universally recovered and comprised 22% of the isolates. The pseudomonads isolated were primarily nonpigmented varieties. Another commonly isolated species was *Yersinia enterocolitica*, found in almost four-fifths of the grass carp examined. Cold enrichment was not required for the recovery of these yersiniae which when present represented the major isolate. No significant differences in speciation of the facultative anaerobes could be found along the length of the tract or in the fish on the various diets, with the possible exception of *Vibrio* which were only present in fish on the weed diet.

The diet was the source for many of these facultative

TABLE 4. Biochemical activities of isolates from the gastrointestinal tract of grass carp.

Biochemical activity		Number tested	Reaction observed: Number positive	Reaction observed: % positive
Strict anaerobes				
Cellobiase agar (Cellobiose)		150	10	6.6
Starch agar (Amylase)		150	14	9.3
Proteolysis agar (Protease)		150	7	4.6
Skim milk agar (Casease)		150	23	15.3
Tributyrin agar (Lipase)		150	14	9.3
Aeromonas hydrophila				
Cellobiase agar (Cellobiose)	O_2[a]	255	143	56.0
	AnO_2[b]	72	23	32.0
Proteolysis agar (Protease)	AnO_2	107	44	41.0
Skim milk agar (Casease)	AnO_2	72	13	18.0
Tributyrin agar (Lipase)	AnO_2	107	69	65.0

[a]O_2 is aerobic.
[b]AnO_2 is anaerobic.

anaerobes and aerobes. The catfish diet contained an average of 1.9×10^5 bacteria per gram, and the weeds contained between 1.8×10^4 and 2.8×10^5 bacteria per gram on aerobic incubation. The catfish diet contained *Micrococcus* and *Bacillus*, while the weed diet contained *Vibrio*, *Bacillus*, *Aeromonas*, *Pseudomonas*, *Moraxella*, and *Alcaligenes*. Anaerobic incubation yielded no strict anaerobes from the catfish diet, while the weeds contained *Clostridium* and *Bacteroides*. The anaerobic counts of the weeds on BBA and PYGA were $8.3–8.7 \times 10^3$ colony forming units/g wet weight. The tank water contained from 10^3 to 10^5 colony forming units/mL with an average count of 10^4 colony forming units/mL, and *Aeromonas hydrophila*, *Pseudomonas*, *Moraxella*, *Acinetobacter*, *Flavobacterium*, *Yersinia*, *Bacillus*, and *Citrobacter* were recovered at various samplings. This probably reflected the fecal flora of the fish in the tank. Interestingly, on the few occasions when the water count was higher than 10^5 colony forming units/mL, the grass carp displayed overt stress symptoms.

Of the strictly anaerobic bacteria isolated from other fish, *Bacteroides* species were most readily isolated from the goldfish (Table 2). Fusobacteria were the most readily recovered anaerobes from the very low numbers of strict anaerobes in the trout. The clostridia in the trout were identified as *Clostridium tetani* and *Clostridium chauvoei*, both presumably originating in the pelleted diet.

Selected biochemical activities of the various anaerobes and of the predominant facultative anaerobes were examined to provide information on the possible role of these organisms in the digestive processes of the grass carp. None of the strict anaerobes degraded cellulose or carboxymethyl cellulose in the test media used, and only 6.6% metabolized cellobiose (Table 4). Even the more commonly metabolized starch was degraded by only 9.3% of the strict anaerobes. These organisms also displayed minimal activity in the proteolytic and lipolytic test media. *Aeromonas hydrophila* was also unable to degrade cellulose or carboxymethyl cellulose aerobically or anaerobically; however, it was markedly more active utilizing cellobiose than were the strict anaerobes. Of the strains examined, more were active on this substrate with aerobic incubation. The results also reveal that significant numbers of the strains of *Aeromonas hydrophila* were proteolytic and lipolytic under anaerobic conditions.

Discussion

This is the first demonstration that fish can have a resident nonpathogenic anaerobic microflora. These anaerobes were present in significant numbers in the grass carp and in the goldfish, but not in rainbow trout. It is possible that this diversity partly reflects the temperatures employed in the cultivation of the fish, the goldfish and carp being maintained at 18–22°C, while the trout were maintained at 11°C. At this lower temperature the time of passage for lumen material in trout is about 12 h, and the generation time for anaerobic bacteria at this temperature apparently does not allow the organisms to reach the population level required to establish a gut microflora before peristaltic washout occurs. At the higher temperatures of 18–22°C, the generation time of the bacteria will be shortened and so the multiplication rate will outweigh the peristaltic washout and allow an anaerobic microflora to become established.

Many of the anaerobes isolated have not been previously described and may be peculiar to fish, while other species isolated from the carp have been reported as comprising both the normal and pathogenic flora of homeotherms, including man. *Bacteroides fragilis* is one example of a normal gastrointestinal inhabitant of man which is often isolated from clinical infections. Another of the carp species isolated from clinical infections of homeotherms is *Fusobacterium mortiferum* (Sommers 1975). The only anaerobe isolated from clinical infections of fish, *Eubacterium tarantellus*, was not among the *Eubacterium* species isolated from these grass carp.

With few exceptions, the facultative species isolated from the grass carp are similar to those isolated from other freshwater fish (Trust and Sparrow 1974; Horsley 1977). Once again *Aeromonas hydrophila* is predominant and may be the most important facultative

species in the gut of all freshwater fish and in some cases it has been the sole bacterial species present (Trust et al. 1978). Although this is the first report of the isolation of *Yersinia enterocolitica* from the gastrointestinal tract of fish, its presence is not surprising considering the wide distribution of the organism in the aquatic environment (Harvey et al. 1976). The low frequency of isolation of most of the other facultative organisms suggests that in most cases these organisms are transient residents of the fish gastrointestinal tract. This is obviously in keeping with the opinion that the fish does not have a true facultative gastrointestinal microflora.

The role of gastrointestinal anaerobic bacteria in the nutrition of the fish remains unclear. Certainly we found no evidence that the anaerobic bacteria isolated from the grass carp are involved in the breakdown of cellulose. This is not surprising given the relatively fast time of passage of food materials through the tract and the absence of an anatomical area where lumen contents could be held for a sufficient period to allow a microbial fermentation to develop. Also, no apparent change in bacterial speciation was observed between fish on a grass diet and those on pelleted diets. Certainly the techniques employed should have revealed cellulose degradation by the various isolates if it were occurring. The anaerobes isolated would not be able to participate in cellobiose breakdown in the fish gut either. *Aeromonas hydrophila*, the predominant facultative anaerobe, was also unable to utilize cellulose or carboxymethyl–cellulose, but was capable of cellobiose degradation. In fact, the wide ranging nutritional capabilities of this aeromonad probably explains its abundance in the gut of these and other fish. Whether its extracellular enzyme capabilities contribute to the gastrointestinal degradative capacity of the fish cannot be answered at this time but their high numbers would suggest that they are metabolically active in situ. In contrast to *Aeromonas hydrophila*, the biochemical refractivity of the anaerobic isolates would seem to rule them out as contributors.

This study has revealed that a strictly anaerobic population of bacteria can exist in the gastrointestinal tract of fish. Associated with this anaerobic population in the grass carp is a variety of facultative species also commonly isolated from other freshwater fishes. None of the species isolated from grass carp was capable of digesting cellulose. This suggests that the grass carp, when existing on a herbivorous diet, differs from the homeothermic ruminants and herbivores. In the case of the grass carp, large quantities of cellulose containing foodstuff must pass through the animal and the soluble sugars and proteins must be extracted after the pharyngeal teeth of the animal have macerated the plant tissues. The undigested cellulose will then pass out in the feces. If any microbial contribution to fish nutrition occurs, it may be in breakdown of other plant carbohydrates.

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Relative Efficiency of Multifilament and Monofilament Nylon Gill Net Towards Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron[1]

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COLLINS, J. J. 1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. J. Fish. Res. Board Can. 36: 1180–1185.

In the early 1970s Lake Huron fishermen converted their gill nets from multifilament to monofilament nylon web in the lake whitefish (*Coregonus clupeaformis*) fishery. Catch comparisons in the two gears showed that monofilament nets were 1.8 times more efficient (but varied seasonally), resulting in biased commercial catch statistics. The use of monofilament web has probably increased exploitation pressure on whitefish. Both gears selected whitefish of the same size despite stock differences in individual size and shape. Catches in both gears declined during the full moon phase, possibly due to increased net visibility.

Key words: mono–multifilament gillnet efficiency, selectivity, lunar illuminance, *Coregonus clupeaformis*, Lake Huron

COLLINS, J. J. 1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. J. Fish. Res. Board Can. 36: 1180–1185.

Au début des années 1970, les pêcheurs de grand corégone (*Coregonus clupeaformis*) du lac Huron remplacèrent le multifilament par le monofilament de nylon dans leurs filets maillants. La comparaison des captures par les deux types d'agrès démontre que les filets en monofilament sont 1,8 fois plus efficaces (mais accusent des variations saisonnières), ce qui a pour effet de biaiser les statistiques de prises commerciales. L'utilisation d'une nappe en monofilament a probablement entraîné une pression de pêche accrue sur le grand corégone. Les deux agrès capturent des poissons de mêmes tailles, malgré des différences de taille et de forme, selon les stocks. Les prises des deux types d'agrès diminuent en périodes de pleine lune, possiblement à cause d'une plus grande visibilité des filets.

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THIS paper documents the increase in efficiency which has resulted from the conversion during the early 1970s from multifilament nylon to monofilament nylon gill nets in the Lake Huron commercial fishery for lake whitefish (*Coregonus clupeaformis*). This is the first major change in gill netting (except for the use of deeper nets) since multifilament nylon replaced cotton web in the early 1950s (McCombie and Fry 1960).

Catch comparisons of Pacific salmon (*Oncorhynchus* spp.) (Larkins 1963, 1964; Washington 1973) and other marine species (Pristas and Trent 1977) showed that monofilament web was more efficient for only certain species. My objective was to compare the relative efficiencies of mono (monofilament) and multi (multifilament) nylon web for whitefish and associated species using commercial nets that were typical of the fishery. The size structure of catches from different stocks was examined in relation to that predicted by net selectivity studies (Regier and Robson 1966; Hamley 1975) and I show the effect of the gear change on the interpretation of commercial catch statistics which are often used to evaluate stock abundance.

The relation between lunar illuminance and catch rates was examined to determine if greater net visibility during the full moon affected the catching efficiency of both gears.

Materials and Methods

The test nets were 114 mm mesh (stretched measure) and were typical of those used to catch whitefish in the North Channel of Lake Huron in 1972. The nominal twine size of the mono web was 0.23 mm; the multi web was 210 denier consisting of two threads, with 25 strands each. The hanging ratio was approximately 50% (i.e. 100 m of twine on 50 m of side line) to make nets that were 91.4 m long and 30 meshes deep.

The relative efficiency of mono and multi nets was compared both when combined in one gang and when set in separate gangs. In the first test the experimental gang which

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TABLE 1. Number of fish caught in monofilament (mo) and multifilament (mu) nylon gill nets with 13.2 km of each net type set in the North Channel and 18.8 km in South Bay, Lake Huron, in 1972 and 1973. Catch ratio equals mo/mu.

Species	North Channel			South Bay			Grand total		
	mo	mu	Ratio	mo	mu	Ratio	mo	mu	Ratio
Lake whitefish	288	151	1.9	775	447	1.7	1063	598	1.78
Rainbow smelt	50	126	0.4	105	397	0.3	155	523	0.30
White sucker	80[a]	108[a]	0.7	142	253	0.6	222	361	0.61
Longnose sucker	198[a]	98[a]	2.0	20	17	1.2	218	115	1.90
Alewife	47	46	1.0	14	38	0.4	61	84	0.73
Splake	1	0	—	60	69	0.9	61	69	0.88
Burbot	0	0	—	41	40	1.0	41	40	1.03
Others[b]	25	23	1.1	68	69	1.0	93	92	1.01

[a]70% of fish estimated from reported weight.

[b]Other genera and numbers of fish caught were: *Coregonus* spp. (46 fish), *Esox* (37), *Prosopium* (35), *Perca* (26), *Stizostedion* (13), *Ambloplites* (10), *Oncorhynchus* (9), *Cyprinus* (3), *Petromyzon* (2), *Roccus* (1), *Salmo* (1), *Dorosoma* (1), and *Aplodinotus* (1).

was 366 m long consisted of four nets strung together to form alternating panels in a mono–multi–mono–multi configuration. The gang was incorporated into one of a fisherman's regular strings of net which averaged 2100 m in length and its position within the commercial gang varied over time without regard for the type of net (mono or multi) adjacent to it. Nets were set in the afternoon and lifted the following morning in 57 netting trials and were left out for two nights in 15 trials. A total of 13.2 km of each net type was lifted during May–October 1972 in the North Channel of Lake Huron (46°05′N, 83°00′W).

The second test compared catches with gear types set independently of each other during April–November, 1973 in the inner and outer basins of South Bay, Lake Huron (45°38′N, 81°52′W). Using the same type of nets, two 366 m gangs were set overnight 54 times (18.8 km of each gear) at two separate sites (paired sets) and the gear types were alternated between the sites so that the multi gang was set in the location occupied by the mono gang in the previous set.

Same day catches in the two gears were not comparable because whitefish were 66% more abundant at one of each of the paired locations (Chi square test $P < 0.001$). Therefore, mono catches were compared with the most recent multi catches at the same site. For this reason certain lifts were excluded from the mono–multi catch comparisons but were retained in the selectivity analysis without introducing bias. In both tests, mono and multi catches were examined separately. Fork length and weight of each whitefish were recorded and scale samples were taken for age determinations. Location, water temperature, depth, and duration of each set were recorded and water transparency was measured by secchi disc, at 88 lifts in South Bay and 19 in the North Channel.

The relative catch rate of the two gears is expressed as the ratio obtained by dividing either mono catch values by multi catches when effort is equal or mono CUE by multi CUE when effort is not equal (CUE = catch per unit of effort where catch is number of fish and effort is km of net set for one night).

The lunar phase–catch relation was derived from daily catch and effort reports of two North Channel commercial fishermen. A total of 796 multi net lifts made from May to September of 1964 to 1968 was compared with 845 mono net lifts in May–September 1972–76. The latter designation is approximate because some multi nets (less than 20%) were used until 1974. Within each component, CUE (kg of fish per km of net lifted) was computed for the day following a lunar phase event (e.g., full moon) and for each of 3 d preceding and following that event. When phase periodicity was 8 rather than 7 d, data for the day midway between the phases were not included.

Results

The catches (Table 1) were typical of a whitefish fishery in the areas netted. Whitefish dominated the catches, but among the 22 other species taken, the most numerous were: rainbow smelt (*Osmerus mordax*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), alewife (*Alosa pseudoharengus*), splake (*Salvelinus fontinalis* × *S. namaycush*), and burbot (*Lota lota*).

Overall, mono nets were 1.8 times more efficient than multi for catching whitefish but were only equal to or less efficient for the remaining species in the catch (although the pooling of data for both sucker species in some of the catches precludes comment on longnose suckers). Catch ratios for whitefish were essentially the same whether the two materials were joined in alternating panels or were set in separate gangs ($P > 0.10$).

Mono/multi catch ratios for whitefish varied throughout the open-water season, with peaks in May and June for South Bay and North Channel catches, respectively (Table 2), but no consistent seasonal trend was apparent.

CUE values for both gears also varied seasonally and monthly catches in mono nets were significantly higher than multi in South Bay ($P < 0.001$) and the North Channel ($P < 0.05$). Correlation coefficients were not significant between the mono/multi ratios and either CUE (abundance), mean lengths, or depth of sets.

SELECTIVITY FOR SIZE AND AGE

Whitefish length frequency distributions (Fig. 1)

TABLE 2. Seasonal variation in effort, depth of sets, and catches of whitefish in monofilament (mo) and multifilament (mu) gill nets, where CUE equals fish per kilometre of net lifted.

	North Channel (1972)						South Bay (1973)					
		Mean depth		CUE		mo/mu		Mean depth		CUE		mo/mu
Month	Effort[a]	(m)	C.V.	mo	mu	ratio	Effort	(m)	C.V.	mo	mu	ratio
Apr.	—	—	—	—	—	—	0.73	8.0	0.0	126.0	90.4	1.39
May	0.55	4.2	10.9	18.2	14.5	1.25	3.66	8.0	0.0	64.8	19.4	3.34
June	1.83	6.0	58.2	23.0	5.5	4.18	2.20	8.0	0.0	5.0	5.0	1.0
July	5.30	15.4	16.6	21.3	9.1	2.34	2.93	41.8	6.7	33.8	21.8	1.55
Aug.	5.12	16.1	11.7	16.8	11.5	1.46	3.66	48.3	19.6	28.1	17.2	1.63
Sept.	2.38	11.8	12.2	12.2	8.8	1.38	0.0	—	—	—	—	—
Oct.	0.73	7.0	24.3	11.0	6.8	1.62	2.74	18.2	35.8	35.8	19.3	1.85
Nov.	—	—	—	—	—	—	2.93	9.7	26.2	46.1	40.6	1.13
Overall	15.91	13.1	34.7	18.1	9.5	1.90	18.85	22.2	77.6	41.11	23.71	1.73

[a]km of each gear type lifted, effort doubled for two night sets in North Channel.

were essentially the same for fish caught in mono and multi web in the North Channel ($P > 0.10$, based on numbers of fish) and in South Bay ($P > 0.50$). When mono and multi catches were combined, the South Bay fish lengths (mode of 43 cm) were smaller than those (45 cm mode) of the North Channel ($P < 0.001$).

The age structure of the catches was examined because visual acuity and net avoidance behaviour may change with age. The age compositions (Fig. 2) of fish from the two gears were also similar in the North

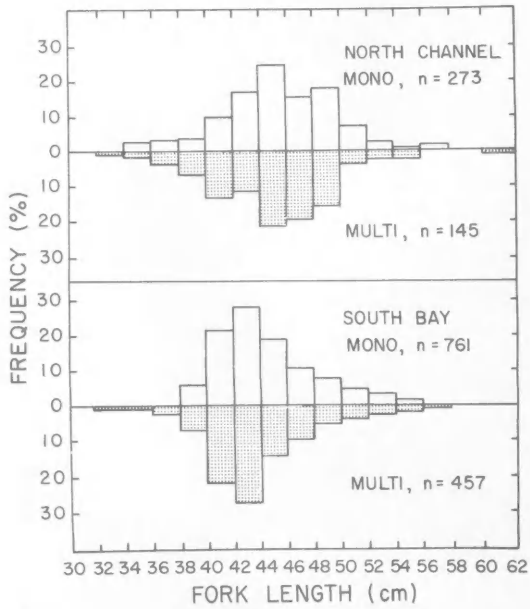

FIG. 1. Length-frequency distributions of whitefish taken in 114-mm mono and multi gill nets in the North Channel (1972) and South Bay (1973), Lake Huron.

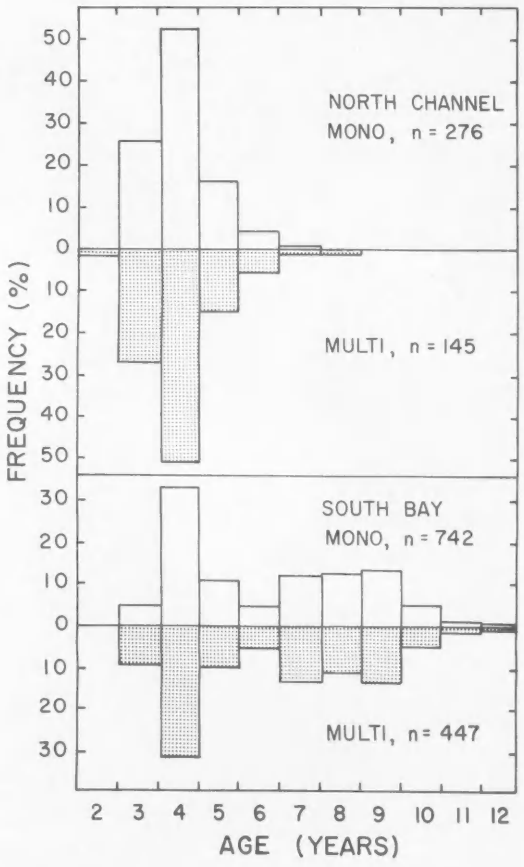

FIG. 2. Age-frequency distributions of whitefish taken in 114 mm mono and multi gill nets in the North Channel (1972) and South Bay (1973), Lake Huron.

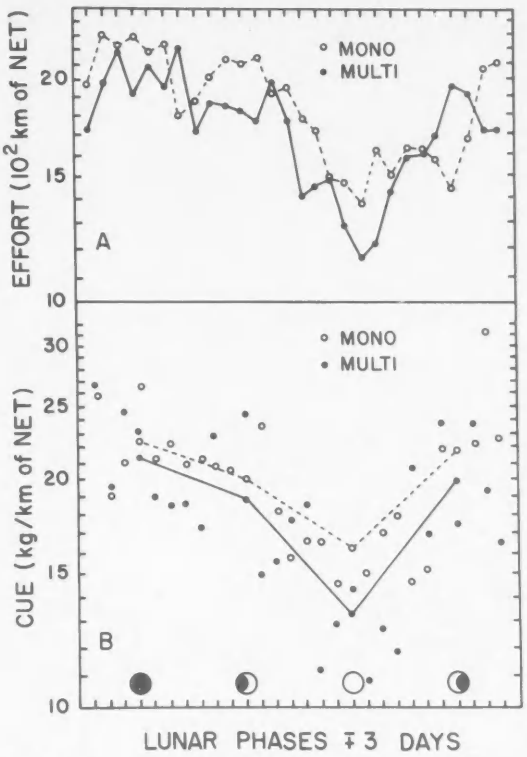

FIG. 3. Trends in fishing effort (A) and CUE (B) in relation to lunar phases. Solid circles and lines represent the multi gillnet period, 1964–68. Open circles and dashed lines represent the mono period, 1972–76.

Channel ($P > 0.50$) and South Bay ($P > 0.10$), but in the latter, the age distribution was bimodal.

Monofilament nets were superior despite differences in size and growth rates of fish available for capture. North Channel data (Fig. 1 and 2) suggest that the nets sampled a stock which recruited to the gear at age 4 (average length, 45.9 cm). Two stocks were apparent in South Bay, one which recruited at age 4 and the other at ages 7–9. Of these, 97.5% of fish age 6 and younger were captured in the outer basin of South Bay and are a migrant stock from Lake Huron (J. C. Budd, J. B. Smith, and F. E. J. Fry, 1963, unpublished report). Their average lengths at ages 3, 4, 5, and 6 were 41.0, 43.6, 48.4, and 51.2 cm, respectively. In contrast, most fish age 7 and older were inner basin stock which grew much slower as average lengths at ages 7, 8, 9, and 10 were 41.3, 42.1, 43.1, and 44.3 cm, respectively. Based on a stratified subsample of 5 fish/cm interval, length–weight regressions and estimated weights of 450 mm fish were:

North Channel

$$W = 1.2984 \times 10^{-5} \times L^{3.0118}, \text{ 1271.6 g;}$$

South Bay, outer basin

$$W = 7.0018 \times 10^{-6} \times L^{3.1089}, \text{ 1241.5 g;}$$

South Bay, inner basin

$$W = 1.6305 \times 10^{-5} \times L^{2.9620}, \text{ 1178.3 g.}$$

where W is weight in grams and L is fork length in mm. Inner basin whitefish were significantly lighter for their length than those from the outer basin (covariance analysis, $F = 11.042$, 1,186 df, $P < 0.01$).

Relation of Lunar Phases to Catches

In the commercial fishery, average whitefish CUE (Fig. 3B) declined during the full moon phase in both the multi net period ($F = 8.911$, 24, 3 df, $P < 0.01$) and the mono period ($F = 4.657$, 24, 3 df, $P < 0.05$) suggesting that lunar illuminance affects catch rates. Fishing effort was also reduced when the moon was full (Fig. 3A).

Discussion

Although the overall catch of whitefish was 78% higher in monofilament net, the mono/multi catch ratio varied over time. Seasonal variation was also reported for catch comparisons of Pacific salmon (*Oncorhynchus* spp.) by Washington (1973) and Larkins (1963, 1964) and the former attributed part of the variation to relationships between effort, abundance and size of fish available for capture. However, these factors were not found to be significant in this study, nor was any relation found between mono/multi ratios and seasonal changes in depth of sets (Table 2) or water transparency (secchi disc values ranged from 4.0 to 10.0 m with maxima occurring in midsummer).

In contrast, monofilament nets were less efficient for rainbow smelt and white sucker, two species that fishermen attempt to avoid when fishing for whitefish. Smelt, which became entangled by their teeth, in the twisted strands of multifilament web were less vulnerable to capture in the single strand mono web which was also less supple. The reason(s) for reduced catches of white sucker are not understood.

Net selectivity for size of whitefish was the same for both gears even though several stocks, each with different growth parameters, were sampled. This result differs from Washington's (1973) observation that Pacific salmon caught in mono net were generally slightly larger.

The modal length of whitefish caught in the North Channel (45 cm Fig. 1) was the size taken most efficiently by 114 mm mesh gillnets (Regier and Robson 1966). Although the majority of fish caught in South Bay were smaller and some were slimmer (and less vulnerable to the gear), the mono/multi ratio was not significantly lower and, in fact, the CUE was considerably higher (Table 2). North Channel fish recruited to the gear at age 4 while fish in the outer basin of South Bay recruited at ages 4–5 and inner basin fish had not attained optimum size by age 10.

A difference in selectivity for age was not apparent

in these data. While selectivity primarily acts upon fish size and shape (Hamley 1975), net perception and net avoidance responses could change with age. Visual acuity may have improved as fish size increased (Hester 1968), and if gillnet avoidance is learned, older fish may have been more adept at avoiding multi nets than the newly introduced mono nets. Hunter and Wisby (1964) showed that fish in a laboratory situation learn to avoid moving barrier nets.

The decline of whitefish catches in both gears during the full moon phase is an unexpected result. If net visibility is the primary factor, catches should have declined less in the transparent monofilament net than in the multi net which by comparison is opaque. Some Lake Huron fishermen have recognized that moonlight affects catches and consequently fish less during the full moon period (Fig. 3A). Catches of trout (*Salmotrutta* f. *lacustris*) in floating nets in Lake Neuchâtel also declined during the full moon period (Quartier 1975). Increased illumination of nets would seem to be the most tenable reason for declining catch rates. However the decline may simply result from reduced fish activity caused by changes in light levels (Lawler 1969; Ryder 1977).

Maximum lunar illuminance at the water's surface is about sevenfold brighter for full moon at the zenith (0.2 lx) than at quarter phases. (Austin et al. 1976). Blaxter and Parrish (1965) estimated that the minimum threshold light level for net avoidance by herring (*Clupea harengus*) was 0.006 lx and in one instance when surface light intensity was about 0.2 lx, sufficient light for net avoidance penetrated ocean water to a depth of 25 m. If the visual sensitivity of whitefish is similar to that of herring, they may be able to see nets set at considerable depths on moonlit nights.

The low visibility of mono web was recognized early as the chief reason for its superior catching power (Molin 1953). Steinberg (1964) showed that net visibility in clear water influences catch efficiency and that the threshold value of visibility differs with species. Accordingly, if the spectral sensitivity and visual acuity of whitefish were known, the question of net visibility could be addressed directly.

Management Implications

The introduction of monofilament nylon web has increased netting efficiency for whitefish and, in the absence of some compensatory constraint, has intensified the exploitation pressure. Concern about dealing with such changes to ensure both conservation of the stocks and maintenance of the fishery was expressed by Christie (1978). Concomitantly, improved gear efficiency has introduced a bias in commercial catch statistics which, if used to evaluate stock abundance, should be adjusted by a correction factor similar to that proposed by Cucin and Regier (1965) where the product of (efficiency factor) × (reported effort) resulted in a corrected effort value termed Effective Effort

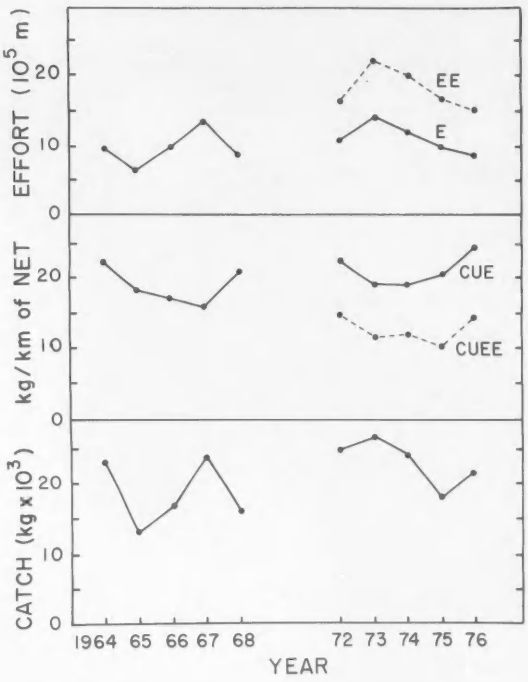

FIG. 4. Comparison of commercial catch (lower panel), CUE (middle panel) and effort (upper panel) in multi 1964–68 and mono periods 1972–76. Solid lines represent raw data and dashed lines corrected data (see text).

(EE). The CUE was computed using EE to yield a corrected CUE value, (CUEE), which is more representative of annual abundance over a period of gear change. Clearly, the raw CUE values since the introduction of mono web, yield a 78% overestimate of whitefish abundance when compared to CUE from multi web. To account for the phasing in of mono web, the correction factor is arbitrarily increased as follows: 1972, mo/mu ratio, 1.5; 1973, 1.6; 1974, 1.65; 1975–76, 1.78.

Using catches from the moon phase analysis, the catch, CUE and effort in the multi net period (1964–68) and the mono period (1972–76) fluctuate but there appears to be little difference between them if gear changes were disregarded (Fig. 4). However, the increased gear efficiency represented by the CUEE values indicates that fewer fish were vulnerable to the gear in the 1970s than in the 1960s. Biological variables which might cause this apparent decline such as changes in growth rate, recruitment age, and relative year-class size must be examined in detail for correct interpretation.

This study shows that in South Bay gill nets caught fish which did not fit the net particularly well and thus, as pointed out by Christie (1978), a large mesh size

does not necessarily protect a stock from over fishing unless effort is also controlled. Clearly, if management is to have a biological basis, individual strategies may be required for each stock.

The introduction of mono web was part of a long series of technological improvements which have occurred in these fisheries (Berst and Spangler 1973) and are continuing to occur. In 1977, some fishermen increased the depth of their whitefish nets from the usual 30–36 meshes to 50 meshes and increased fishing power has undoubtedly resulted which may be more important than the change in web.

Gear improvements must be continually evaluated if management decisions are based on catch statistics and where whitefish stocks are stressed by intensive exploitation, some control over the use of more efficient gear is warranted. Mechanisms for appropriate surveillance and response are proposed in the new management strategy for Ontario fisheries (Loftus et al. 1978).

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Olfactory Bulbar Electrical Responses of Rainbow Trout (*Salmo gairdneri*) Exposed to Morpholine During Smoltification

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HARA, T. J. AND S. B. BROWN. 1979. Olfactory bulbar electrical responses of rainbow trout (*Salmo gairdneri*) exposed to morpholine during smoltification. J. Fish. Res. Board Can. 36: 1186–1190.

Exposure of rainbow trout (*Salmo gairdneri*) to 5.7×10^{-10} M (5×10^{-5} mg/L) morpholine during smolting period did not influence the subsequent neural response to this substance, when tested immediately and 12 mo after smolting. No significant difference in the morpholine-induced responses was obtained between the exposed and unexposed fish. Using *N*-ethylmaleimide, a sulfhydryl reagent, it was further confirmed that the morpholine-effect is caused by a mechanism not directly associated with the normal olfactory function. Perfusion of the olfactory organs with 1.0×10^{-1} and 1.1×10^{-1} M (1%) morpholine for 10 min irreversibly inhibited the olfactory responsiveness to odorants. Sensitization of the olfactory bulbar electrical response is discussed in connection with homing of morpholine-imprinted salmonid fishes.

Key words: olfaction, olfactory bulbar response, rainbow trout, salmon, imprinting, morpholine, homing, migration

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L'exposition de truites arc-en-ciel (*Salmo gairdneri*) à $5{,}7 \times 10^{-10}$M (5×10^{-5} mg/L) de morpholine au moment de la smoltification n'influence pas la réaction neurale subséquente quand on les expose à cette substance immédiatement ou 12 mois après smoltification. On n'observe pas de différence appréciable dans les réponses déclenchées par la morpholine chez des poissons exposés et non exposés. A l'aide de la *N*-éthylmaléimide, un réactif sulfhydryl, nous avons pu nous assurer que l'effet morpholine est produit par un mécanisme qui n'est pas directement lié à la fonction olfactive normale. La perfusion des organes olfactifs avec $1{,}0 \times 10^{-1}$ et $1{,}1 \times 10^{-1}$ M (1%) de morpholine durant 10 min bloque de façon irréversible la réponse olfactive aux substances odoriférantes. Nous analysons la sensibilisation de la réponse électrique du bulbe olfactif en fonction du «homing» de salmonidés de morpholine.

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RECENT studies on morpholine-imprinted coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Salmo gairdneri*), and brown trout (*Salmo trutta*) led Hasler and his colleagues to conclude that these fish can imprint to morpholine, retain this information until the spawning migration, and use it to identify a stream scented with this chemical (see review by Hasler et al. 1978). This conclusion is supported by their extensive ultrasonic tracking and census studies on homing fish (Cooper and Scholz 1976; Cooper et al. 1976; Scholz et al. 1976, 1978). Also support for this conclusion is based on the fact that significant differences were obtained in the magnitude of the induced electroencephalographic (EEG) response to 1% (1.1×10^{-1} M) morpholine for the fish exposed to 5×10^{-5} mg/L (5.7×10^{-10} M) morpholine as fingerlings as compared to the fish not exposed to morpholine (Cooper and Hasler 1974, 1976; Dizon et al. 1973). This has raised two important issues regarding imprinting. Can fish be imprinted olfactorily to any chemical present in water, and is this imprinting electrophysiologically demonstrable in terms of the sensitization of olfactory bulbar responses to chemicals? Some of their electrophysiological studies, particularly the use of high concentrations of morpholine, were later criticized by Hara (1974) and Hara and Macdonald (1975), who, characterizing EEG responses induced by morpholine in rainbow trout, concluded that the morpholine-effect observed with high concentrations was probably caused by a mechanism which is not directly associated with the normal olfactory function. However, the central theme of the criticism seems to have been incorrectly understood (Cooper and Hasler 1976; Leggett 1977).

The present study was undertaken to characterize further the nature of the electrical responses induced in the olfactory bulb by nasal infusion of morpholine

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and a standard stimulant (L-serine) in two groups of rainbow trout. One group was exposed to morpholine and one unexposed, in an attempt to determine whether simple exposure to low concentration of a chemical produces any electrophysiologically measurable sensitization. The effect of high concentrations of morpholine as an inhibitor of olfactory function was also studied in comparison with the effects of a sulfhydryl reagent, *N*-ethylmaleimide.

Materials and Methods

Two groups of 35 rainbow trout (*Salmo gairdneri*) fingerlings were held in laboratory tanks supplied with a continuous flow of dechlorinated tap water (10 ± 0.5°C; pH 7.3–7.6). The photoperiod was adjusted to 12 h light and 12 h darkness. One group was exposed to morpholine when the fish were 11 mo old. Exposure continued until the trout showed color changes associated with smoltification (loss of parr marks and silvering) 5 mo later. The other group was left unexposed to serve as a control. The concentration of morpholine used to treat the fish was 5.7×10^{-10} M (5×10^{-5} mg/L). This is the same concentration that was originally employed by Cooper and Hasler (1974). The fish were tested twice in electrophysiological experiments. Ten fish from each group were examined immediately after smoltification, and five each were examined 12 mo after completion of smoltification (the total of 18 mo after morpholine treatment started). During this period their mean body length increased from 14.9 to 20.6 cm at smoltification and to 32.4 cm 12 mo after smoltification. The number of the olfactory lamellae remained unchanged (14–18 lamellae versus 15–18 lamellae).

The electrical responses were measured in the olfactory bulb when the nares were stimulated with chemical solutions according to methods described previously (Hara 1977a). Solutions of L-serine (10^{-5} M) were used as standard stimulants throughout, and the stimulatory effectiveness of each chemical was estimated relative to the mean response to this standard at the beginning, during, and at the end of each experiment. In toxicity experiments, the olfactory organs were treated with morpholine and *N*-ethylmaleimide (NEM), a sulfhydryl (SH)-alkylating reagent, by infusing solutions into nasal cavities for 10 min. Infusion was done by the same method described previously (Hara et al. 1976), except that, in the present study only the nares were infused. Stock solutions of chemicals were made with distilled water and stored in a refrigerator. The final test solutions were freshly prepared, just prior to each application, with the same water that perfused the gills and nares. Morpholine (purified) was obtained from Fisher Scientific Co.

Results

Morpholine-Induced Response

Typical responses to L-serine and morpholine are illustrated in Fig. 1. When the nares of fish were infused with 10^{-5} M L-serine solution, the background electrical activity of the olfactory bulb was immediately (in the order of ms) interrupted by an oscillatory potential (induced response) that was terminated by rinsing. With morpholine at 1.0×10^{-1} and 1.1×10^{-1} M (1%; same concentration that was originally employed by Cooper and Hasler), the background activity slowly increased and returned to the original level slowly after prolonged rinsing. The response normally started 6–7 s later than did the L-serine response, and as long as 1 min was required for complete recovery (bottom record, Fig. 1). At 10^{-2} and 10^{-3} M, the effect of morpholine was primarily a brief inhibition of the spontaneous background activity. No response was recorded with morpholine at 10^{-4} M and lower (Fig. 2).

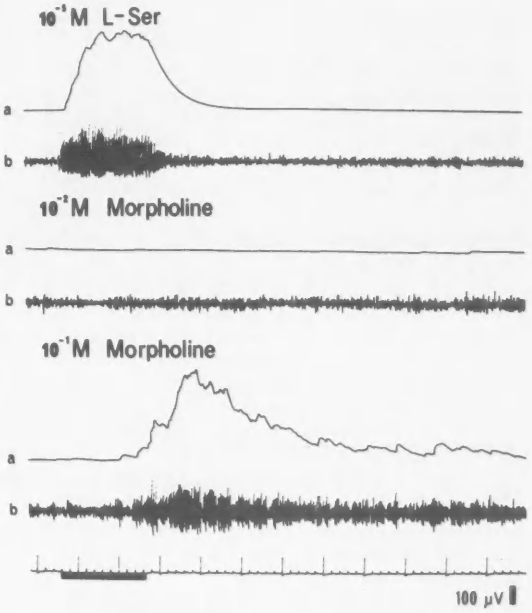

FIG. 1. Typical olfactory bulbar responses induced by L-serine and morpholine. Note a long delay in the morpholine reaction. This effect gradually builds up and reaches maximum after cessation of stimulus, and sustains over a longer period even after rinsing. Upper traces (a) in each pair show integrations of the lower (b). A heavy line at the bottom indicates the duration of the stimuli. Time scale, 1-s divisions.

Exposure to morpholine during the smolting period did not influence the subsequent neural response to the stimulants when tested immediately after and 12 mo after the completion of smoltification. There was no significant difference in responses between morpholine-exposed and unexposed groups both to L-serine (*t*-test, $P > 0.2$ at 10^{-4} M) and morpholine (*t*-test, $P > 0.2$ at 1.1×10^{-1} M) over the concentration ranges tested (Fig. 2).

The mean pH values of 1.1×10^{-1} M morpholine solutions was 10.5 (range, 10.4–10.6) in the present study. The response to 1.1×10^{-1} M morpholine decreased considerably when the pH of the solutions was lowered by addition of 1 N HCl solution (Fig. 3). At

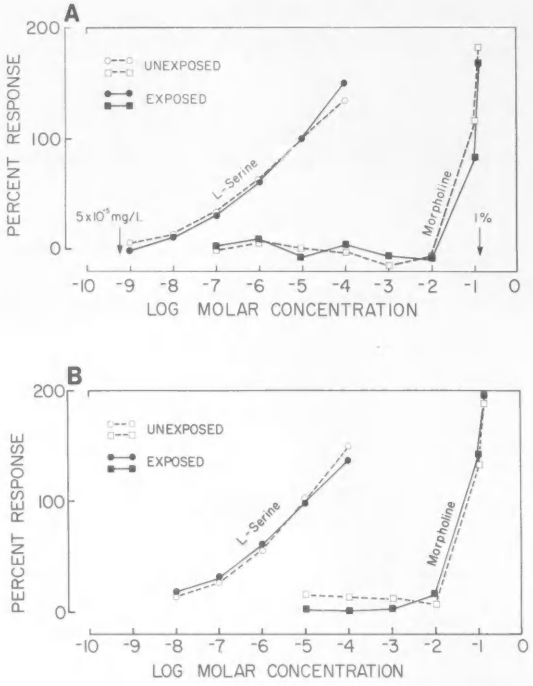

FIG. 2. Comparison of the bulbar responses to L-serine and morpholine between the group exposed to 5.7×10^{-10} M morpholine and the group not exposed. A, immediately after smoltification, and B, 12 mo later than A. The percent response in this and next figures is calculated relative to the response to the standard stimulant 10^{-5} M L-serine. Concentrations of 5×10^{-5} mg/L and 1% are indicated by arrows. Responses below the base line at 10^{-2}–10^{-3} M indicate the inhibition of the spontaneous activity.

these pHs, typical morpholine responses were abolished, and a L-serine type response, probably due to the excess of HCl, was induced.

EFFECTS OF NEM ON THE RESPONSES INDUCED BY MORPHOLINE AND OTHER STIMULATORY COMPOUNDS

NEM at 10^{-4} irreversibly inhibited the L-serine response (Fig. 4). The response did not return to the original level by normal rinsing. Similar to L-serine, the responses, to L-alanine, D-serine, skin mucous substance, and food extract were inhibited by 10^{-4} M NEM. In contrast, the responses by 1.0×10^{-1} M morpholine were augmented, after a brief initial depression, during treatment with NEM at 10^{-4} M. The response remained slightly depressed after rinsing (Fig. 4).

INHIBITION BY MORPHOLINE OF THE BULBAR RESPONSE

Perfusion of 10^{-2} M morpholine into the nares for 10 min reversibly inhibited the L-serine response (Fig.

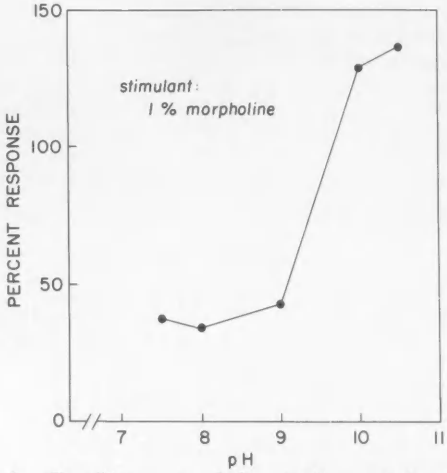

FIG. 3. The pH-response relation of 1% morpholine. The pH is adjusted by concentrated HCl solution.

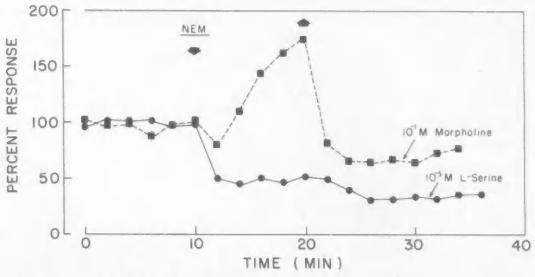

FIG. 4. Effects of *N*-ethylmaleimide, a sulfhydryl-alkylating reagent, on the bulbar responses induced by 10^{-5} M L-serine and 1.0×10^{-1} M morpholine. Arrows delimit the period of treatment. The percent response in this and next figures is calculated relative to the response immediately before treatment.

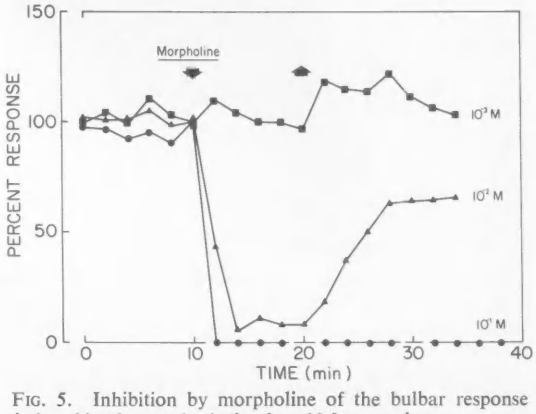

FIG. 5. Inhibition by morpholine of the bulbar response induced by the standard stimulant 10^{-5} M L-serine.

5). The response slowly returned to the normal level after rinsing. Morpholine at 1.0×10^{-1} and 1.1×10^{-1} M inhibited the response irreversibly. The fish no longer responded to odorants, though the background electrical activity remained at the similar level as that of the normal. Perfusion of morpholine solutions at these concentrations was characterized by an initial strong response lasting for about 1 min, then the background activity slowly returned to the normal level.

Discussion

The present study wholly confirmed our previous reports (Hara 1974; Hara and Macdonald 1975). All fish tested gave a large, long-delayed and long-lasting response to 1.0×10^{-1} and 1.1×10^{-1} M morpholine, which is distinct from the response induced by odorants such as food extracts, hand rinse, and amino acids (Hara 1975). This suggests that morpholine, instead of acting at specific receptor sites on the membrane, may penetrate into the olfactory epithelium and cause a nonspecific irritational effect at nonspecialized cell surfaces. In humans and experimental animals, morpholine is an effective surface-active and emulsifying agent, irritating eyes, skin, and mucous membranes (Merck Index, 8th ed., 1968). The surface of the olfactory mucosa of vertebrates is covered with a layer of mucus which forms a reservoir of inorganic ions needed for the electrical events associated with sensory transduction (Bannister 1974). Because the mucus consists mainly of mucopolysaccharides and lipoproteins (Herberhold 1968), it is probably subject to surfactant action. Temporary depression of the L-serine response by 10^{-2} M morpholine could be due to removal of the mucus layer which undergoes continuous renewal. Permanent loss of responsiveness at higher concentrations may be the results of destruction of the specific membrane structures, or total cell damage.

Morpholine is strong base with a pK_b of 9.61 (Merck Index, 8th ed., 1968). It is impossible to adjust the pH of 1.1×10^{-1} M morpholine solution without considerable change in the ionic strength. The response to 1.1×10^{-1} M morpholine sharply drops when the pH is lowered beyond its pK_b. Cooper and Hasler's (1974, 1976) data support this; no response was induced by buffered morpholine solutions. Ionization of morpholine is likely to be a requirement for its characteristic effect. Olfactory response is pH dependent in rainbow trout; responses to odorants are inhibited below pH 3 and above pH 9 (Hara 1976; Hara and Macdonald 1976). It is not likely that the olfactory transduction process can take place at such a nonphysiological pH as 10.5.

It is generally assumed that protein and lipid in the receptor membranes form the probable receptor molecules for chemical stimuli and that binding of stimulant molecules is translated into permeability changes by means of a conformational change in proteins. Various group-specific reagents have been known to react with protein side-chain groups and disrupt functioning of nerve cells. In chemosensory systems, application of group-specific agents eliminates or reduces electrical or behavioral responses in rat, frog and insect. NEM specifically inhibits responses to L-serine, hand rinse and food extracts, indicating the involvement of SH-groups in olfactory transduction in this species (Hara et al. 1976; Hara and Brown unpublished data). The morpholine effect, on the contrary, was augmented under the influence of NEM, suggesting a mechanism which is not directly associated with the normal olfactory function.

Exposure of nonmigratory rainbow trout to morpholine at 5.7×10^{-10} M during their smolting period did not influence the subsequent neural response to morpholine or L-serine for up to 12 mo. In migratory salmonids, exposure to morpholine caused olfactory sensitization which could be detected 10 mo (Dizon et al. 1973) and 18 mo later (Hasler et al. 1978) using electrophysiological methods. The rainbow trout that were electrophysiologically examined in the present study may not have been in spawning condition, consequently the fish were unable to show increased sensitivity to the chemical. However, all our experimental fish responded with high intensity to 1.1×10^{-1} M morpholine. No fish failed to respond to morpholine at such a high level, thereby suggesting that the effects of the chemical were nonspecific. In contrast, other studies (Cooper and Hasler 1976) have shown that nonexposed salmon exhibited low responses to morpholine at 1.1×10^{-1} M. The sensitization observed in migrating salmonids may be due in part to nonspecific effects caused by increased levels of serum steroid hormones during spawning. It is known that the spontaneous and evoked olfactory bulbar electrical responses are augmented by injection of estradiol in goldfish (*Carassius auratus*) (Oshima and Gorbman 1966, 1968, 1969; Hara 1967). Moreover, the sensitization due to imprinting may not be detectable by simple comparisons of the bulbar responses to morpholine with those to a standard substance (NaCl or amino acids), because the salmon should have been imprinted differentially to the standard substances as well. Amino acids and inorganic ions are ubiquitous and present in natural waters at concentrations exceeding that of morpholine used (Burnison 1971). Thus, salmon could be imprinted to virtually any chemical present in water during a critical period. If this is the case, it would follow that the olfactory bulbar responses to all natural occurring substances are generally greater in adults than in juveniles.

Although homing of salmonids artificially imprinted to a low level of morpholine is evident from extensive behavioral studies (cf. Hasler et al. 1978), the involvement of olfaction in the imprinting to morpholine at 5.7×10^{-10} M has never been established. Electrophysiologically, no homing coho salmon responded to concentrations of 1.1×10^{-2} and 1.1×10^{-3} M morpholine (Cooper and Hasler 1974, 1976). In the present

study, morpholine produced no olfactory response before the concentration reached 10^{-3} M where it rather caused inhibition of the background electrical activity. Furthermore, a recent heart-rate conditioning study by Hirsch (1977) has shown that coho salmon is not able to detect morpholine olfactorily at concentrations lower than 2.3×10^{-8} M. This does not necessarily mean that the fish are unable to detect the chemical, because electrophysiological and conditioning techniques may not be sensitive enough to record a response. Nevertheless, the same electrophysiological method has been universally employed to measure high sensitivity of the fish olfactory system to other chemical stimuli such as amino acids (cf. Hara 1975). The threshold thus measured is often only slightly higher than that determined behaviorally (Hara 1977b). Chemical imprinting and subsequent homestream recognition could have occurred via sensory channels (gustatory and general chemical sense) other than olfactory. To solve this problem, the following experiments will have to be carried out; 1) a group of salmon fingerlings with their nose cauterized are to be exposed to low level of morpholine before down stream migration, and 2) migrating adult fish with their nose cauterized are to be released and ultrasonically tracked through a morpholine plume again.

In conclusion, we found no electrophysiological evidence indicating nonmigratory rainbow trout could detect morpholine olfactorily at concentrations lower than 10^{-4} M. Further, we failed to obtain any electrophysiological evidence to indicate that nonmigratory rainbow trout can imprint olfactorily to morpholine; exposure of rainbow trout to morpholine at 5.7×10^{-10} M had no influence on the subsequent neural response to morpholine.

Acknowledgments

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Impact of Brook Trout (*Salvelinus fontinalis*) Predation on the Crayfish *Orconectes virilis* in Three Michigan Lakes[1]

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GOWING, H., AND W. T. MOMOT. 1979. Impact of brook trout (*Salvelinus fontinalis*) predation on the crayfish *Orconectes virilis* in three Michigan lakes. J. Fish. Res. Board Can. 36: 1191–1196.

The crayfish *Orconectes virilis* is a major component of the benthos of three small lakes in northern Michigan. These lakes contained stocked brook trout (*Salvelinus fontinalis*) populations (age-0 and age-I) at densities of 188, 411, and 1398 fish/ha. Crayfish were preyed upon by brook trout, but only during their first year of life. Two-year production of age-0 crayfish was approximately 94 kg in each lake; brook trout consumed only about 1–2% in lakes with lower density of fish. Even with greater trout density and accompanying higher rate of exploitation (40%), there was no impact on recruitment of young crayfish because compensatory mortality of crayfish occurred in lakes with less trout predation. However, stocking trout at higher densities decreased trout growth and condition. While 2-yr production was highest (59 kg/ha) in the lake stocked at the highest density and lowest (17 kg/ha) in one stocked at the lowest density, the former was achieved at the cost of a very slow growing trout population. Most of the crayfish production is not utilized as trout food but enters the non-predatory pool of detrital organic matter.

Key words: Orconectes virilis, brook trout, predation, production growth, mortality

GOWING, H., AND W. T. MOMOT. 1979. Impact of brook trout (*Salvelinus fontinalis*) predation on the crayfish *Orconectes virilis* in three Michigan lakes. J. Fish. Res. Board Can. 36: 1191–1196.

L'écrevisse *Oronectes virilis* est un élément important du benthos de trois petits lacs du Michigan septentrional. Ces lacs contiennent des populations introduites d'ombles de fontaine (*Salvelinis fontinalis*) (âges 0 et I) à des densités de 188, 411 et 1 398 poissons/ha. Les écrevisses servent de proies aux ombles de fontaine, mais seulement durant la première année de leur existence. La production de 2 a d'écrevisses d'âge 0 est d'environ 94 kg dans chaque lac; les ombles de fontaine ne consomment qu'environ 1–2% dans les lacs à densité moindre de poissons. Même avec une plus forte densité d'ombles de fontaine et le taux d'exploitation plus élevé (40%) qui s'ensuit, le recrutement de jeunes écrevisses ne change pas, car dans les lacs où la prédation par l'omble de fontaine est moins forte, il y a mortalité compensatrice des écrevisses. Cependant, le peuplement d'ombles de fontaine à de plus fortes densités ralentit leur croissance et affecte leur condition. Alors que la production de 2 a est maximale (59 kg/ha) dans le lac ayant reçu le peuplement le plus dense et minimale (17 kg/ha) dans le lac à densité de peuplement moindre, la production plus grande fut réalisée au dépens d'une croissance très lente de la population d'ombles de fontaine. La plus grande partie de la production d'écrevisses n'est pas utilisée comme nourriture par l'omble de fontaine, mais contribue au pool de détritus organiques non soumis à la prédation.

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THE crayfish *Orconectes virilis* is a major component of the benthic biomass of marl lakes in Northern Michigan (Momot et al. 1978). In this report we assess the fraction of production by crayfish in three lakes that is passed on to brook trout (*Salvelinus fontinalis*), the major secondary consumer stocked in these lakes at different densities.

Three lakes (North Twin, South Twin, and West Lost) which lie in the karst topography of the north-central lower peninsula of Michigan are classified as limestone sink lakes. Their morphometry is similar: small in area; subcircular in outline; steeply cone-shaped in form with a narrow littoral area; and comparatively deep (Table 1). Additional limnological features are

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TABLE 1. Physical and chemical characteristics of three sink lakes.

Lake	Surface area (ha)	Depth (m)		Percent shoal[a]	Average total alkalinity (mg/L)	pH (mean)	Specific resistance[b] (ohms/cm³)
		Maximum	Average				
North Twin	1.9	12.5	5.6	13.0	29.2	7.4	20 900
South Twin	1.6	10.1	5.9	15.3	65.2	7.8	8 400
West Lost	1.4	13.1	6.0	11.0	134.4	8.0	4 156

[a]Water less than 1.2 m
[b]Corrected to 25°C.

given by Tanner (1960) and Momot and Gowing (1972). The limited aquatic vegetation consists mainly of yellow water lily, *Nuphar variegatum*, and the sedge *Carex aquatilus* var. *substricta*.

These are characteristic marl lakes with typically high transparency, low organic matter, and a paucity of aquatic vegetation. Benthic algae accounts for most of the photosynthesis (Hooper and Ball 1964), whereas phytoplankton is low (Raymond 1937). Production of insects is limited by lack of aquatic plants (Wohlschlag 1950; Berg 1949).

The lakes differ primarily in alkalinity, lime being precipitated only in the most alkaline lake. Their productivity is similar based on summer standing crops of benthic invertebrates (Siler 1968) and growth attained by brook trout stocked at the same size and density (Latta 1967). In general, however, rates of production are considered low for all trophic levels (Wetzel 1970).

Materials and Methods

Trout populations were maintained in these lakes by annual stockings of fall fingerling brook trout. In October of 1965, residual stocks of brook trout in these lakes were composed of from two to four year-classes, but mostly the 1964 year-class. In early November 1965, the lakes were stocked with young-of-the-year brook trout (1965 year class) that ranged between 127 and 152 mm in total length (averaged 142 mm) and each weighed about 29 g. The fish were fin clipped for identification. Events leading to the establishment of stock densities of brook trout at the outset of this study are summarized as follows:

Lake	Residual stocks Oct. 1965	Number stocked Nov. 1965	Stock density established
North Twin	62/ha	240	188/ha
South Twin	168/ha	390	411/ha
West Lost	149/ha	1750	1398/ha

In the spring and fall of 1966 and 1967, estimates of the trout population were made by the Petersen mark-and-recapture method, following the field procedure recommended by Waters (1960). In the fall trout were captured by angling and nets, marked by excision of a fin, and released. The population was again sampled using electrofishing gear to obtain a ratio of marked to unmarked fish to derive an estimate. In the spring the methods of capture were generally reversed. Mortality rates and production were calculated following Ricker (1975).

Growth and other features of the trout populations were based on monthly samples of trout of the 1965 year-class collected from each lake, mainly by angling and infrequently by electrofishing and gill nets. Generally, five trout per month were removed from North Twin, and about 10 per month from South Twin and West Lost lakes. In addition, monthly samples also included, when possible, five larger fish from the 1964 year-class from all lakes. Further, the occasional older trout (1963, 1962, and 1961 year-classes) captured during the sampling period, were retained. All trout collected were used for diet studies.

Between December 1965 and October 1967, 152 brook trout were removed from North Twin, 246 from South Twin, and 275 from West Lost Lake for examination of diet. Trout examined ranged in length from 130 to 370 mm.

For the analysis of diet, items in the stomach contents were identified, counted, and volume determined by water displacement. Gastric evacuation of food from the stomach varies with water temperature and the kind (taxa) of food consumed (Hathaway 1927; Hess and Rainwater 1939; Phillips et al. 1960; Molnar and Tolg 1962; Brett and Higgs 1970; Noble 1972). Therefore, the observed diet was adjusted for differential evacuation rates related to temperature and taxa as proposed by Alexander (1977) and Alexander and Gowing (1976). For this study, we equated 1 mL to 1 g weight (Ball 1948).

The monthly consumption of crayfish by trout was derived in the following manner. First, the number of crayfish per stomach was determined from the monthly sample of trout. This ration was then multiplied by the mean size of the trout population to provide the number of crayfish consumed per day. The daily consumption was multiplied by a temperature and taxa factor, and finally by the number of days in a month to obtain the monthly consumption of crayfish.

The monthly mean size of the trout population was determined on the assumption that mortality rates were constant between spring and fall and between fall and spring and therefore the population size between seasons can be extrapolated from logarithmic plot of spring and fall estimates.

Estimates of the population size of young crayfish (hatchlings) in June were derived as a product of the number of adult breeding females times the mean number of attached eggs per female (Momot 1967a). Estimates of population size of yearlings and adult crayfish were made during the spring and fall of 1966 and 1967; and those for young-of-the-year were made annually in early fall. For

TABLE 2. First-year production of age-0 crayfish and their consumption by brook trout in North Twin, South Twin, and West Lost lakes.

Lake and period	Production (kg)	Number of predators	Consumption by brook trout (kg)
North Twin			
July–Sept. 1966	50.46	144–106	0.08
Oct. 1966–June 1967	37.97	87–19	0.60
South Twin			
July–Sept. 1966	61.64	262–202	0.27
Oct. 1966–June 1967	31.85	173–30	1.38
West Lost			
July–Sept. 1966	60.90	1091–1007	13.68
Oct. 1966–June 1967	38.03	958–395	26.13

the former, the common, round wire minnow trap was the method of capture while hand nets were employed for the latter. Estimates of crayfish were derived by the Schumacher–Eschmeyer formula (Ricker 1975). The methods and techniques involved in obtaining estimates of crayfish population size, age composition, growth, and production are discussed by Momot (1967b) and Momot and Gowing (1977a).

Adult females were sampled with hand nets in the spring when they were carrying eggs attached to the pleopods. Direct counts of attached eggs were made (Momot and Gowing 1977a, b).

Results

CRAYFISH

Brook trout preyed on young-of-the-year crayfish almost exclusively. Estimates of population size of young-of-the-year crayfish were calculated for late June, again in September, and finally in June of the following year at the end of their first year of life. Young-of-the-year crayfish first become available to trout in July, shortly after being shed by the female, at a carapace length of about 6 mm. In September they have reached a length of approximately 14 mm, and by June of the following year have attained a length of about 22 mm which approaches the upper size limit of crayfish eaten by brook trout of the size present in these lakes.

The sequence of estimates of standing crops of young-of-the-year crayfish beginning in early summer and ending one year later are summarized as follows:

	Standing crop (kg)		
Lake	June (1966)	Sept. (1966)	June (1967)
North Twin	7.62	40.17	21.95
South Twin	6.62	48.41	19.39
West Lost	22.48	32.99	17.78

The standing crop of crayfish hatchlings in West Lost Lake at the outset was more than three times larger than in North Twin and South Twin lakes. However, the total mortality rate of young crayfish during the summer was highest in West Lost Lake, 0.84 compared to 0.60 and 0.61 in North Twin and South Twin. As a result, the standing crop of young crayfish in West Lost at the end of summer dropped below that in North Twin and South Twin. In the following 9 mo total mortality rates were similar (0.84–0.88). Consequently, standing crops of young crayfish after 1 yr were of the same magnitude.

In general, production of young-of-the-year crayfish in each lake was comparable (Table 2). Between 57–66% of the annual production was made during the summer and 33–43% during the balance of the year.

TROUT

The populations of brook trout present in the three lakes in November 1965, were all substantially reduced by fall 1967. Trout densities at the outset were 188 fish/ha in North Twin, 411 fish/ha in South Twin, and 1398 fish/ha in West Lost. In North and South Twin lakes about two-thirds of these populations were comprised of brook trout of the 1965 year-class and one-third brook trout of the 1964 year-class, whereas in West Lost Lake 89% were of the 1965 year-class and 9% belonged to the 1964 year-class. By October 1967, these populations had diminished to about 5 fish/ha in North Twin and South Twin lakes and 149 fish/ha in West Lost Lake. The reduction in population size during the 2 yr was, in part, due to our scheduled removal of trout; monthly samples of trout represented 42% of the initial stock in North Twin, 37% in South Twin, and 14% in West Lost.

Stocking density affected growth, condition and production of trout. In the overall range of 188–1398 fish/ha at the outset, there was an apparent inverse relationship between density and growth. For the 1965 year-class brook trout in North Twin, the 2-yr increment in growth was 191 mm and 529 g, in South Twin 165 mm and 359 g, and in West Lost 89 mm and 122 g. For this period the overall coefficient of condition (K) was 1.09 in North Twin, 1.00 in South Twin, and 0.95 in West Lost. Tuunainen (1970) and Johnson and Hasler (1954) have also reported an inverse relation-

TABLE 3. Estimated biomass (B) and production (P), in kilograms, of the 1965 year-class and all year-classes of brook trout combined, in North Twin, South Twin, and West Lost lakes between November 1965 and October 1967. ($\bar{B}$ is mean biomass from 2 adjacent yr).

Lake and date	B Year-class		P Year-class		$P/\bar{B}$
	1965	All	1965	All	
North Twin					
Nov. 1965	6.92	24.44	1.58	2.18	
Apr. 1966	6.67	14.15	16.25	21.97	
Oct. 1966	13.39	19.97	1.30	2.27	1.09
Apr. 1967	4.72	5.60	6.14	6.14	
Oct. 1967	5.58	5.58		—	0.66
			Total	32.56 (17.14 kg/ha)	
South Twin					
Nov. 1965	11.24	47.14	3.42	4.04	
Apr. 1966	11.56	22.96	18.98	25.04	
Oct. 1966	18.45	28.32	0.00	0.21	0.77
Apr. 1967	7.33	7.93	4.86	5.23	
Oct. 1967	3.31	4.02		—	0.34
			Total	34.52 (21.58 kg/ha)	
West Lost					
Nov. 1965	50.45	78.24	3.93	10.31	
Apr. 1966	31.18	37.98	40.36	41.34	
Oct. 1966	61.46	63.66	3.40	3.40	0.73
Apr. 1967	40.12	40.12	27.80	27.80	
Oct. 1967	31.50	31.50		—	0.66
			Total	82.85 (59.18 kg/ha)	

ship between density and growth for brook trout and salmonids stocked in lakes.

Two-year trout production was largest in West Lost stocked at the highest density of trout and smallest in North Twin stocked at the lowest density (Table 3). For West Lost Lake, production was 2.7 times larger than South Twin and 3.4 times larger than North Twin. For all three lakes the annual turnover ratio of the biomass (annual production divided by the mean standing crop) was largest the first year and diminished the second year. In the first year the largest turnover ratio occurred in North Twin and in the second year North Twin and West Lost showed similar ratios, both exceeding that found in South Twin.

TROUT DIET

Nine orders of insects were represented in the diet of brook trout from all lakes. However, the four most important insect orders by weight were: Diptera, primarily tendipedid larvae and to a lesser extent *Chaoborus*; Hemiptera, mostly corixids and some notonectids; Odonata, both dragonfly and damselfly larvae in the ratio of about 3 to 1; Coleoptera, largely dytiscid adults and gyrinids. Of the Crustacea found in the stomachs, only two were important: Decapoda (specifically *Orconectes virilis*) and Cladocera (specifically *Daphnia galeata mendotae*). This assemblage of six orders of organisms is the basis for the comments on the diet of trout.

From an examination of the seasonal food habits of trout, using the 12 mo of 1966, two aspects of the trout diet were common to all three lakes (Table 4). First, insects, largely dipterans, made a relatively large contribution to the diet of trout in the spring; second, cladocerans most commonly entered the trout diet in fall and winter. Trout in North and South Twin relied basically on a diet of insects through most of the year, increasing their use of cladocerans during the fall and winter. Crayfish played a minor role and were seasonally variable. These two lakes differed primarily in that cladocerans made a greater contribution to the diet of trout in South Twin than in North Twin. In contrast, trout in West Lost relied mostly on crayfish throughout the year with cladocerans playing the principal supporting role during the fall and winter and insects during the spring only.

To facilitate comparisons with results obtained in an earlier brook trout predation study by Momot (1967a), we used two size categories for calculation of predation rates, <229 mm in total length and ≥ 229 mm. These were based on the length distribution of trout in the monthly samples and on fish sampled in the spring and fall.

TABLE 4. Seasonal composition of brook trout diet (grams per stomach), adjusted for temperature and taxa, in three lakes. (Temperature factor: Winter — December–March, 0.70; Spring — April, 0.84 and May–June, 1.00; Summer — July–August, 1.00; Fall — September–October, 1.00 and November, 0.77).

Lake and season	Order and taxa factor					
	Diptera 0.86	Hemiptera 0.25	Odonata 0.21	Coleoptera 0.17	Cladocera 1.32	Decapoda 0.84
North Twin						
Winter	—	0.069	0.001	0.004	0.075	0.049
Spring	0.132	0.002	0.022	0.002	0.010	0.118
Summer	0.071	0.022	—	0.002	0.046	0.029
Fall	0.979	0.031	0.008	0.008	0.021	0.083
South Twin						
Winter	—	0.013	0.004	0.006	0.086	0.010
Spring	0.181	0.003	0.005	0.001	0.038	—
Summer	0.067	0.022	—	0.001	0.017	0.046
Fall	0.080	0.004	0.005	0.002	0.051	0.011
West Lost						
Winter	0.002	0.001	0.001	0.000	0.037	0.199
Spring	0.035	0.010	0.003	0.006	0.001	0.048
Summer	0.025	0.002	—	0.001	0.031	0.141
Fall	0.004	0.001	0.000	—	0.070	0.146

Brook trout in both North Twin and South Twin cropped a very small portion of age-0 crayfish production in their respective lakes when densities ranged between 164 to 10 fish/ha. Of the production of crayfish in North Twin and South Twin, trout predation accounted for less than 2% (Table 2). However, at the comparatively higher trout density (779–282 fish/ha) in West Lost, about 40% of young crayfish production was utilized.

Discussion

Brook trout are littoral oriented. Only young-of-the-year crayfish are consumed by brook trout and they first become available to trout in late June or early July. Most young-of-the-year crayfish are initially found in the immediate shore area, but as summer progresses their range increases.

A primary concern in trout management centers on whether the stocking of trout at high densities can cause severe enough predation to affect the survival of their prey. In this study brook trout at the highest density (779–282 fish/ha) cropped the largest fraction of the production of young crayfish. Despite this higher rate of exploitation by brook trout in West Lost, there was no evident decrease in recruitment of age-0 crayfish to the population. Trout predation, in effect, acted as a compensatory form of mortality in that trout ate crayfish that would have died of other causes. Compensatory mortality occurred in North Twin and South Twin lakes as residual stocks of young crayfish, after their first year of life, were of the same magnitude in both lakes and comparable to West Lost Lake. Evidently, trout predation had no impact on the crayfish population.

On the other hand, stocking density did have a profound impact on trout populations. The high density of trout in West Lost Lake resulted in intense intraspecific competition for food. This competition was reflected by the relatively poor growth and condition of trout in West Lost Lake compared to North Twin and South Twin lakes. Additional evidence of this competition is shown by the 9–13% average loss in weight by brook trout of both year-classes during the winter of 1965–1966. These data suggested that trout were forced to feed on young crayfish, an abundant and available source of sustenance. In this instance, the high density of 1965 year-class trout, coupled with their comparatively good survival, resulted in little more than maintenance of the stock. In effect, trout production was achieved by a relatively large number of trout each attaining a small increment in weight. On the other hand, the ratio of cohort production to weight of fish stocked was highest for the 1965 year-class trout in North Twin (2.6) and lowest in West Lost Lake where first year production was less than the weight stocked.

In an earlier study, Momot (1967a) reported on the utilization of crayfish by brook trout in West Lost Lake. The density and structure of the trout population were similar to the brook trout population in South Twin in the present study. He concluded that brook trout consumed only young-of-the-year crayfish, only trout $\geq$229 mm consumed crayfish, and about 7% of the annual production of young-of-the-year crayfish was utilized.

We achieved increased utilization of crayfish by stocking trout at higher density. Also, at high density small trout ($<$229 mm) in competition for food readily

consumed crayfish. Under less stressful conditions in West Lost Lake in 1962–1963 and in North Twin and South Twin lakes during 1966–1967 in the present study, small trout (<229 mm) did not utilize crayfish even though they were abundant. The trout population that survived in West Lost Lake in our study showed an unacceptable rate of growth of individual trout and would provide an unsatisfactory sport fishery.

Crayfish in these lakes represent a large source of energy for possible conversion into trout flesh. However, this is not the ultimate fate of these crustaceans but instead most enter the non-predatory pool of detrital organic matter largely through decomposition by microorganisms. Similarly, the same fate befalls zooplankton (Wetzel 1975).

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Tidal Energy and Sublittoral Macrobenthic Animals in Estuaries

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WILDISH, D. J., AND D. D. KRISTMANSON. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. J. Fish. Res. Board Can. 36: 1197–1206.

A quantitative hypothesis is presented that current velocity and roughness at the sediment–water interface control the numbers, biomass, and growth of suspension-feeding macrobenthic animals. The controls are the effect of tidal currents on turbulent mass transfer of food to suspension-feeding animals and direct inhibition of growth and settlement by currents in excess of 12–30 cm/s. The rate of turbulent supply of ATP associated with seston is proposed as a practical way of determining growth potentials of suspension-feeding macrobenthos at current velocities less than 30 cm/s.

Key words: sublittoral macrobenthos, tidal velocity, potential population growth, Bay of Fundy estuaries

WILDISH, D. J. AND D. D. KRISTMANSON. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. J. Fish. Res. Board Can. 36: 1197–1206.

Les auteurs avancent une hypothèse quantitative voulant que la vitesse du courant et la rugosité de l'interface sédiment–eau règlent le nombre, la biomasse et la croissance des animaux benthiques qui se nourrisent de matière en suspension. Les facteurs de contrôle sont l'effet des courants de marée sur le transfert turbulent en masse de la nourriture vers les animaux se nourrissant de matière en suspension et l'inhibition directe de la croissance et de la sédimentation par des courants dépassant 12–30 cm/s. Ils proposent la vitesse d'apport turbulent d'ATP associé avec le seston comme moyen pratique de déterminer le potentiel de croissance du macrobenthos se nourrissant de matière en suspension à des vitesses de courant inférieures à 30 cm/s.

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TROPHIC group analysis of sublittoral macrobenthic communities of estuarine or marine particulate substrates shows that two key groups are present: suspension and deposit feeders. Suspension feeders filter seston, here defined as inorganic or organic particles greater than 0.8 μm diameter suspended in the water, whereas deposit ingesters indiscriminantly or selectively ingest particles that are part of the sediment profile. In their trophic group amensalism hypothesis, Rhoads and Young (1970) suggested that biogenically resuspended sediment, produced by the action of deposit ingesters, inhibits suspension feeders by clogging filtering mechanisms and also that unstable sediment does not provide a suitable substrate for larval settlement. An alternative to this, the trophic group mutual exclusion hypothesis proposed by Wildish (1977), suggests that both groups are food limited and that the basic exclusion mechanism involves a physical factor, the turbulent mass transfer of seston. Current velocity and bottom roughness are considered to be the factors that control the supply of suspended food (see also Sanders 1956; Krumbein 1971), and current velocities greater than a few centimetres per second inhibit the development of the deposit ingesting community by removing biogenically resuspended sediment and by controlling the rate of exchange of limiting substances across the sediment–water interface.

The purpose of this paper is twofold: firstly, to present a quantitative hypothesis with which to examine hydrographic parameters and food supply as possible limiting factors in the development and growth of suspension feeding macrobenthic animals, and secondly, to present some field data designed to test some assumptions and that part of the trophic group mutual exclusion hypothesis applicable to suspension feeders.

Theory

Near the sediment–water interface the movement of water is restrained by its contact with the bottom. In this region, a boundary, or Ekman layer develops (Wimbush and Munk 1970) whose characteristics are determined by the velocity of the bulk flow and the roughness of the sediment–water interface. In all practical cases the Ekman layer is turbulent except for a region a few centimetres above the bottom. The thickness of the Ekman layer is of the order of 1 m and depends on the current velocity.

The construction of a quantitative hypothesis that the supply of food to suspension feeders is controlled by the same physical factors which regulate supply of seston re-

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quires several assumptions. The supply of seston must be dependent on the mean current velocity and bottom roughness. The trophic value of seston to suspension feeders must be represented by particulate ATP and be evenly distributed throughout the bulk of the bottom 2 m of the water column at the point where observations are made. Finally the suspension feeding animals must occupy a large areal proportion of the tidal excursion.

The concentration of ATP-seston, C^* pg/m^3, at the sediment–water interface must be less than the bulk concentration in the water column, C pg/m^3, when ATP-seston is being consumed. The rate at which ATP-seston is transferred to suspension feeders at the sediment–water interface, N_A pg·m^{-2}·s^{-1}, is sustained by turbulent mass transfer:

$$(1)\quad N_A = k(C - C^*)$$

where k is a mass transfer coefficient (Sherwood et al. 1975) in m/s. In a steady state situation for a given value of C and the same suspension feeding consumption rates, the value of C^* will be low if mass transfer is weak and high when mass transfer is more energetic. Estimates of k may be made from the rate of momentum transfer to the boundary of the flow, that is from the Fanning friction factor, f. The Chilton–Colburn analogy relates the mass transfer coefficient to the friction factor, the mean velocity and two fluid properties:

$$(2)\quad k = V\frac{f}{2}\left(\frac{D}{\nu}\right)^{2/3}$$

where V = mean tidal velocity 1–2 m above the sediment–water interface in m/s
D = molecular diffusivity of the entity transferred
ν = kinematic viscosity.

The bracketed term allows for a region near the interface in which molecular diffusion is the dominant transfer process. However, the pumping action of many suspension feeders, or an hydrodynamically rough bottom, reduces the importance of molecular diffusion and it is more appropriate in this case to ignore the contribution of molecular diffusion to the transfer process and write as a first approximation:

$$(3)\quad k = V\frac{f}{2}$$

The friction factor may be obtained from a knowledge of the shear stress at the bottom, τo, as measured by several investigators (Sternberg 1968; Harvey and Vincent 1977). Sternberg (1968) measured a term equivalent to a friction factor at six locations in the Strait of Juan de Fuca and Pugent Sound. The bottom shear stress was related to the friction factor by

$$\tau o = \frac{1}{2}fpV^2, \text{ or } \tau o = C_d pV^2$$

where V is the current velocity 1 m above the bottom, p is the fluid density, and C_d is the drag coefficient related to the velocity 1 m above the bottom. The locations varied from hydrodynamically transitional to rough, and also in sediment type, but the friction factor only varied twofold over a wide range of flow rates with little dependence on V. If this is so, it is reasonable to write equation (3) as

$$k = V\gamma$$

where γ is a dimensionless coefficient which depends only on bottom roughness. Using this relationship the mass transfer equation (1) becomes:

$$(4)\quad N_A = \gamma V(C - C^*)$$

where γ is $\simeq 3 \times 10^{-3}$, the exact value being related to the bottom shear stress. Equation (4) is applicable only to an hydrodynamically rough flow and if a significant laminar layer exists near the bottom a correction is made by applying the molecular diffusivity adjustment of equation (2). More elaborate treatments for significant resistance to transfer in the laminar and turbulent regions are available (Sherwood et al. 1975). Because little is known about bottom roughness and the "molecular diffusivity" of ATP-seston their use in our approach would be of limited value.

The relationships given above can be used to analyze the feeding of suspension-feeding animals when they are limited by mass transfer processes. Hence, the rate at which ATP-seston is transferred to a specific population of suspension feeders, P the individuals/m^2, is:

$$(5)\quad N_A = R\alpha C' P$$

where R is the average pumping rate per individual, m^3/s, and α the filtering efficiency of the animal as a proportion of the maximum possible and ranging from 0 to 1. C' is defined here as the ATP-seston concentration just sufficient to meet the ration maintenance requirements of the population of suspension feeders without allowing significant positive or negative growth. The dependence of growth on ration has been studied in mussels, *Mytilus edulis* (see Widdows et al. 1979) where a minimum maintenance as well as an optimum ration resulting in maximum possible growth has been described. C' will tend to adjust either by animal death or following a period of positive or negative growth, to a concentration which will allow the ATP-seston demand by suspension feeders to be met by turbulent mass transfer, i.e.:

$$(6)\quad N_A = \gamma V(C - C')$$

Combining (5) and (6), an estimate of mass transfer limited population density, P, is obtained:

$$(7)\quad P = \frac{\gamma V}{R\alpha}\frac{(C - C')}{C'}$$

This relationship can be used to determine whether mass transfer limitation of ATP-seston is a feasible hypothesis for population growth and this is attempted later in the paper.

Materials and Methods

Water

Samples were taken at hourly intervals from an anchored 20-m research vessel during one complete tidal cycle (12–13 h) at each sample location. Seven locations (Table 1), in five different estuaries opening into the Bay of Fundy, were investigated. Positioning of the vessel during sampling was based on shore landmarks and hence accurate to within 50 m. Each location was sampled four times during 1975–76: in fall (November/December), winter (February/March), spring (June), and summer (August). Samples were taken in a Nansen reversing water bottle which was cleansed but not sterilized before use. A surface sample, 1–2 m below the surface, and a bottom sample, 1–2 m

TABLE 1. Position of sample locations in Bay of Fundy estuaries.

Location	Name	Position	
		Lat. N	Long. W
1	Saint John Harbour #7	45°15.0′	66°03.5′
2	Musquash Estuary #6	45°11.2′	66°15.3′
3	Digdeguash Estuary #1	45°09.9′	66°57.6′
4	L'Etang Inlet #4	45°04.8′	66°48.0′
5	L'Etang Inlet #11	45°06.0′	66°47.7′
6	St. Croix Estuary #5	45°07.0′	67°07.0′
7	St. Croix Estuary #10	45°09.0′	67°09.0′

above the sediment, were taken at each location for each sampling time (given as Atlantic Standard Time to the nearest 15 min). Seawater was collected in 200-mL glass bottles which had previously been tap washed and, just before use, rinsed with excess of seawater. Temperature was measured immediately with a mercury bulb thermometer, read to 0.1°C and accurate to 0.5°C.

To determine microbial ATP, aliquots were taken with a plastic disposable syringe and passed through a Swinnex filter holder fitted with a Millipore filter (HAWP 02500) having a nominal pore size of 0.45 μm. The assembled Swinnex filter was stored sterile in aluminum foil. The filtrate volume was measured until 15 mL were obtained, then discarded and the 0.45 μm filter removed and placed in a sterile, graduated pyrex vial containing 2 mL of tris buffer (0.02 M tris (hydroxymethyl) aminomethane in deionized, sterile water adjusted with HCl to pH 7.8). After boiling in a sand bath for at least 2 min, the sample was stored on ice until returned to the laboratory. Here the filter was removed, the volume of tris extract recorded and the sample stored at −20°C until analyzed. The remainder of the seawater sample was returned to the laboratory for further analyses.

Current velocities at surface (1–2 m) and bottom (1–2 m above the sediment) were measured at hourly intervals just after the water samples were taken with a current meter (Ott C 31-00) set to integrate over 100-s periods. Current velocities are given in centimetres per second (cm/s), the minimum sensitivity obtainable being 1.6 cm/s.

Adenosine 5′-triphosphate (ATP) was determined on the thawed extracts by the "optimum sensitivity" method (Wildish 1976a). The following analytical conditions were used:

- — Source of the luciferin–luciferase: E. I. Dupont, de Nemours & Co., Wilmington, Delaware 19898, USA, with 3 mL deionized water/vial. For spring and summer samples of 6 mL/vial were used to obtain adequate sensitivity and to minimize cost.
- — Laboratory temperatures of 25 ± 2°C.
- — 0.2 mL luciferin–luciferase solution 0.2 mL of unknown or standard ATP.
- — ATP concentrations were calculated from peak height light emission data.

Sensitivity limits under these conditions were better than 0.5 ng/L and reproducibility near this concentration within ±10% (±2 × SE). Three possible systematic errors were investigated during this work as follows:

Sediment inhibition — During transfer of the 0.45-μm filter some suspended sediment or seston was carried into the tris extract where it could inhibit light emission. Model experiments showed this effect to be minimal with the quantities involved.

Salt inhibition — The 0.45-μm filter transfers 50–100 μL of seawater to the tris extract. Tests with ATP standards and sterile seawater ($S = 30‰$) show that 40–50% inhibition results. The effect is salinity dependent but, because salinities at all locations were near 30‰, a 45% increase has been applied to all the data. Dilution was not a suitable way to correct for this effect because greater than 5× dilution for salinity-inhibited ATP standards caused enhancement of activity.

Interference from non-adenylate nucleotides — The peak height measure of the light emission decay curve, which occurs within 2–3 s after injection, was used to calculate ATP concentrations. Because of this and because purified luciferin–luciferase reagents were employed, no interference from adenosine diphosphate or other non-adenylate nucleotides, which may be converted to ATP by transphosphorylating enzymes present in the crude preparation, was present during light emission and thus no enhancement of activity resulted (Wildish 1976a).

Suspended solids were determined, in bottom seawater only, after thoroughly shaking the bottle and filtering through a 0.8-μm matched weight filter (Millipore AAP0470M) and measuring the volume of filtrate. After drying overnight and weighing, to 0.1 mg, the weight of the lower was subtracted from the weight of the upper filter. Results are expressed as mg solids/L to the nearest 1 mg/L. The UV absorbance at 250 nm was measured on the filtered sample in 1-cm cuvets with distilled water as reference.

Salinity (*S*‰) was measured with 5-mL aliquots by argentometric titration with International Standard seawater from Charlottenlund, Sweden, as standard and is accurate to 0.5‰.

SEDIMENT

Ten replicate Smith–McIntyre grab samples were taken during the summer at each location for characterization of the macrofauna after sieving through a 1-mm² mesh. These samples were obtained as part of a sampling program designed for estuarine resource management purposes (Wildish 1976b, 1978a; Wildish et al. 1977, 1978) unconnected with the present study. Taxonomic identification, enumeration, and wet weighing of preserved samples were carried out either by the Canadian Oceanographic Identification Centre, Ottawa, or the Identification Centre, St. Andrews. Data were analyzed by ecological analytical techniques described previously (Wildish 1978b). Sediment subsamples were taken from the 0.1-m² Smith–McIntyre grab. Dried subsamples were analysed for sediment sorting characteristics by dry sieving for the sand fraction and sedimentation rate analysis of the silt/clay fraction (Akagi and Wildish 1975). Organic carbon was determined by the Walkley and Black method (Akagi and Wildish 1975) and organic matter by combustion at 550°C for 15 min and expressed in each case as percent dry weight of sediment.

Results

CHARACTERIZATION OF SAMPLE LOCATIONS

The maximum depth sampled was 35 m at high water (Table 2). Three of the locations in Table 1 (numbers

TABLE 2. Physical properties of sea water (mean of four seasonal values each with 13 hourly observations) 1–2 m above the sediment–water interface.

Location	Depth at HW (m)	Tidal current, cm/s			Salinity ‰	Temperature °C		Suspended solids, mg/L	A250 nm × 10^3
		mean	min.	max.		min.	max.		
1	12	32.0	6.1	71.2	24.8	?	17.2	29.6	96
2	15	38.0	1.6	126.1	24.3	0.8	17.7	77.8	60
3	8	9.3	<1.6	47.9	30.0	1.1	16.0	19.9	14
4	20	9.0	<1.6	36.4	31.6	1.7	14.5	7.8	26
5	12	27.5	<1.6	100.4	30.9	−0.7	16.3	13.5	112
6	35	15.5	<1.6	44.5	31.3	?	15.0	27.4	16
7	25	18.7	<1.6	57.9	30.4	0.5	15.0	22.0	23

2, 3, and 5) are close to land and protected on all sides so that little fetch was available to develop wave-induced motion near the bottom. Of the others, location 1 (Saint John Harbour) is open to winds from the east to north, the most seaward L'Etang location, number 4, is open to the south and the two St. Croix Estuary locations (6 and 7) are open in a narrow sector to the south. Mean tidal current velocity is high at three locations (1, 2, and 5 in Table 2). Mean salinities reflect the degree of mixing with river water at each location and correlate with the maximum/minimum temperature. This is because seawater conserves heat whereas river water follows ambient air temperature, thus resulting in a wider temperature fluctuation where salinity is lower. Suspended solids range from 8 to 30 mg/L except in the Musquash estuary where the high value (77.8 mg/L) reflects the inorganic and organic particles in the latter derived from the *Spartina* marsh plant detritus brought down by the strong tidal ebb currents (Wildish 1978a). Considerable seawater absorption at 250 nm, an approximate indicator of dissolved organic carbon, occurred at locations 1, 2, and 5. As indicated by the shape of the UV spectral curves, the high values for locations 1 and 5 are caused by pulpmill effluents (Wildish et al. 1976). Location 2 values are associated with dissolved organic carbon resulting from mineralization of marsh plant detritus. Slightly elevated mean values of UV absorption for locations 4 and 7 indicate much diluted pulpmill effluent at these locations.

TABLE 3. Summary of sediment sorting and organic carbon data in Bay of Fundy estuaries. MDϕ = median particle phi value, QDϕ = phi quartile deviation and SKqϕ = phi quartile skewness.

Location	MDϕ	QDϕ	Skqϕ	Carbon as % of sediment dry weight	% volatile solids
1	5.39	0.63	+0.01	0.50	—
2	0.30	2.38	−2.13	0.04	1.10
3	7.94	0.79	−0.13	3.11	—
4	1.87	3.46	+2.24	0.88	0.91
5	7.82	2.51	+1.65	2.35	1.80
6	6.75	3.02	−1.12	2.55	6.44
7	7.40	2.01	−0.26	2.03	5.92

Four stations have soft sediments with most of the particles in the silt/clay size range (Table 3). Of these only location 3 may be classified (see Swift et al. 1973) as well sorted.

Mean particulate ATP levels (Table 4) in the seawater near the sediment–water interface at the seven locations range from 88 to 628 ng/L, a sevenfold difference. The higher ATP values correlate approximately with high UV absorbance values.

The sublittoral benthic communities at the seven study locations may be characterized biologically as *impoverished*, *mixed*, or *deposit ingesting* (Table 4). Impoverished communities consist of a few species which are trophically deposit feeders and/or predators, of low species diversity and biomass (e.g. locations 1 and 2, Table 5). At four of the locations mixed communities were present which have in common a relatively high species diversity and share representative species of both key trophic groups: suspension feeding and deposit ingesting. Mixed communities may be found where most of the biomass is suspension feeding (e.g. location 5, Table 5) or deposit ingesting (e.g. location 4, Table 5). The community at location 3 is the only one which may be rigorously defined as deposit ingesting, that is, containing species of only one of the key trophic groups although it does have a predator, *Cerebratulus* sp. (4.76 g/m^2). At location 3 species diversity, density, and biomass are relatively low, the latter because the key dominants, *Casco* and *Yoldia*, are small. These dominants produce a highly reworked, pelletized sediment of low density which is periodically resuspended. The forces responsible for this are not known but may be short-lived turbulent eddies as found by Rhoads (1973) in Buzzards Bay due to the effect of wave motion near LW, or to short-lived tidal currents not measured by our current meter.

For mixed communities, which range from primarily suspension to primarily deposit feeding, the definition of the point in the spectrum in which a particular community may be placed should ideally be made by

TABLE 4. ATP of the water column and macrobenthos at the same location. s = number of species, n = number of individuals and α = diversity index (see Wildish 1978b).

Location	Mean ATP (ng/L)			Type	Community			
	Surface	Bottom						
	summer	summer	all seasons		s/m^2	n/m^2	$\alpha \pm 2 \times SE$	g/m^2
1	2167	1026	367	Impoverished	6	73	0.8±0.4	3.60
2	1291	1339	418	Impoverished	3	55	0.4±0.2	2.25
3	669	763	323	Deposit	22	449	5.0±1.2	18.50
4	1369	1238	427	Mixed	35	296	10.0±2.2	99.43
5	791	1487	628	Mixed	17	135	5.0±1.5	154.89
6	255	201	88	Mixed	33	137	13.0±3.6	64.75
7	905	193	172	Mixed	24	200	7.5±2.0	197.77

reference to the proportions of annual production produced by each trophic group. In practical terms, such information will rarely be available and the definition could, less satisfactorily, be made by reference to the relative proportions of biomass or density. Difficulties here are that suspension feeders are typically large (e.g. *Chiridota laevis* and *Cucumaria frondosa* at location 5) while deposit ingesters are typically small (for example the maldanids, protobranchs, and lumbrinereids at location 4).

EFFECT OF TIDES

Tidal flood and ebb currents have marked effects on most of the seawater physical parameters measured. Typical patterns through one tidal cycle are shown (Fig. 1) for the mixed but primarily suspension feeding community at location 5, and deposit feeding community at location 3. For the former (Fig. 1a) tidal currents are quite regular, although asymmetrical because the flood is stronger than the ebb current. Because of seawater dilution the UV values are lowest at full flood and highest at low water. ATP follows quite closely the UV values rather than the generally low suspended solid values. At location 3 (Fig. 1b), on the other hand, the tidal currents are weak and quite asymmetrical. UV values here (not shown) are very low and do not correlate with the ATP concentration. Short-lived ATP peaks seem to be associated with the re-suspension of sediment near low water.

For comparison, the tidal cycle patterns of other mixed communities (Fig. 2) show that they are in some ways intermediate between the extremes just mentioned. Location 4 is closest to the deposit feeding community, because here fine sand resuspension occurs, probably caused in part by tidal current erosion and by wind/wave activity. Tidal currents are low although ATP does not seem to be associated with suspended solids (Fig. 2a). Location 7 is closest to a suspension feeding community where tidal currents are relatively high and the suspended solids concentration (Fig. 2b) is low.

EFFECT OF SEASON

Seasonal variables such as temperature and ATP concentration (Fig. 3) for all estuaries examined are loosely related if a semilogarithmic plot is made the fit

TABLE 5. Biomass dominants as wet weight >1 g/m^2 with total biomass of suspension and deposit feeders in summer. P = polychaete, C = crustacean, N = nematode, H = holothurian, without letter = mollusc.

Location	Suspension feeders	g/m^2	Deposit ingesters	g/m^2
1	—	0	*Nepthys incisca* (P), *Goniada maculata* (P)	2.24
2	—	0	*Nepthys ciliata* (P)	1.40
3	—	0	*Yoldia sapotilla*, *Casco bigelowi* (C) *Ninoe nigripes* (P) *Nepthys incisa* (P), *Micura sp.* (N)	13.74
4	*Crenella glandula*, *Astarte undata*	19.14	*Praxillella praetermissa* (P), *Nepthys incisa* (P), *Lumbrinereis fragilis* (P)	50.39
5	*Cyclocardia borealis*, *Chiridota laevis* (H), *Astarte undata*	129.69	*Nereis virens* (P), *Nepthys* sp. (P)	8.23
6	*A. islandica*, *Astarte* sp., *C. borealis*	36.42	*Ophioglycera gigantea* (P), *Yoldia sapotilla*	2.54
7	*C. borealis*, *Mya arenaria* *Mytilus edulis*	183.39	*Ophioglycera gigantea* (P), *Yoldia sapotilla*, *Nepthys* sp. (P)	11.88

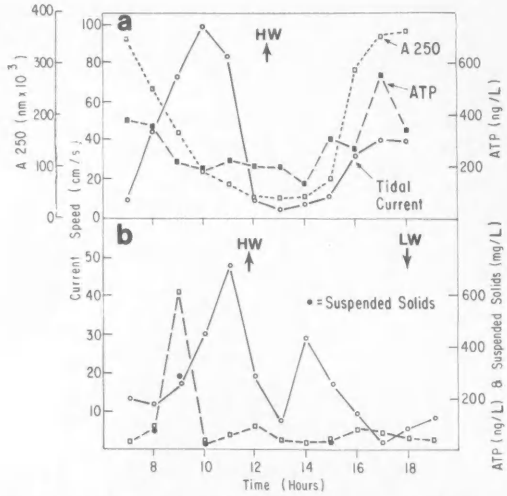

FIG. 1. Tidal effects on ATP (closed squares), absorbance at 250 nm (open squares), suspended solids (closed circles), and current speeds (open circles) 1–2 m above the sediment–water interface. a) Location 5. Upper L'Etang #11 on November 5, 1975; b) Location 3. Lower Digdeguash #1 on November 19, 1975.

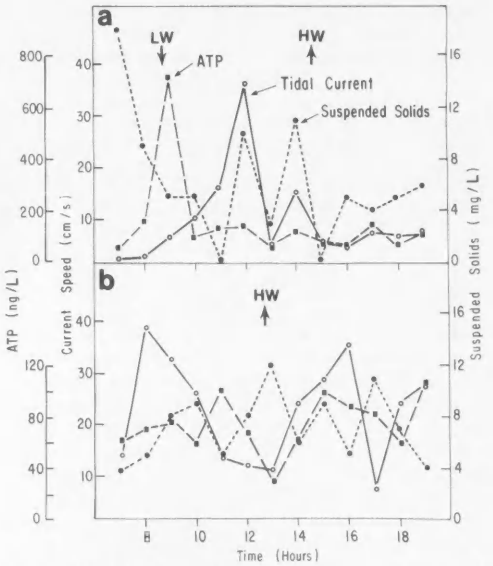

FIG. 2. Tidal effects on ATP (closed squares), suspended solids (closed circles), and current speeds (open circles) 1–2 m above the sediment–water interface. a) Location 4. Upper L'Etang #4 on February 2, 1976; b) Location 7. Lower St. Croix estuary #10 on March 2, 1976.

is log ATP, ng/L = 16 × mean temperature, °C + 0.48, for all spring, summer, and fall data above 6–8°C ($r^2 = 0.53$, $n = 19$). The winter data (range 2.8–5.9°C) do not follow this trend and are suggestive of a specialized, cold-tolerant microflora.

One other parameter showing seasonal variation is dissolved organic carbon. The sample locations shown in Table 6 are grouped according to their degree of pollution by pulpmill effluent: severe, 1 and 5; mild, 4 and 7; unpolluted, 2, 3, and 6. Location 2 in the Musquash estuary drains *Spartina* marshland. Each shows a fall peak of absorbance at 250 nm, indicative of a natural input of dissolved organic carbon. The source is probably decomposing algae and marshland flowering plants that die or shed leaves at this time of year. Microorganisms in estuarine water, as indicated by ATP concentrations, are not active in utilizing this fall pulse of soluble carbon when minimum water temperatures fall below 8.5°C.

GROWTH POTENTIALS

Values for the rates at which ATP-seston are transferred to the sediment–water interface (N_A), assuming $C^* = 0.5C$, were computed as a crude measure of the potential for growth at a given locality (Table 7), based on mean values for tidal velocity (V) and the concentration of ATP-seston (C); the two locations (1 and 2) with impoverished macrobenthic communities have the highest values, followed by the mixed location (5), with the deposit feeding community (3) having a low value. Thus, the communities classified as impoverished are limited by factors other than turbulent supply of seston as will be discussed below.

Discussion

It is evident that multiple physical and biological factors interact to produce the three benthic macrofaunal community types recognized. One key physical factor is the amount of tidal energy characteristic of each sample location (Table 7). Tidal currents influence the turbulent supply of seston to sublittoral bottom suspension feeders as well as cycles of sediment erosion and deposition. Sediment erosion results in an unstable sediment unsuitable for the larger suspension feeders particularly at settlement. It is known (Perkins

TABLE 6. Seasonal effects on dissolved organic carbon as absorbance at 250 nm in arbitrary units, means of tidal observations.

	Locations						
Season	1,	5	4,	7	2	3,	6
Fall	114	162	38	32	99	24	30
Winter	—	57	29	33	55	18	20
Spring	114	100	22	5	40	5	5
Summer	56	118	15	22	44	10	9

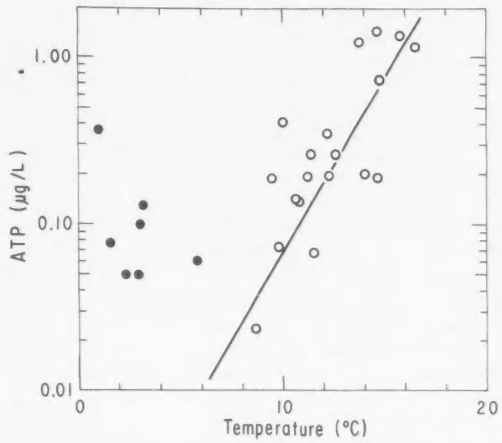

FIG. 3. Effect of temperature as mean values for one tidal cycle (hourly observations/13 h) on mean ATP concentration (hourly observations/13 h) for all locations and seasons. Open circles — spring, summer, and fall, closed circles — winter.

1974) that the critical current velocity causing erosion is 15 cm/s for the most susceptible sand fraction (median particle diameter of 0.10–0.50 mm). Our data (Table 8) show that only at locations 1, 2, and 4 are the tidal velocities sufficient to erode the sediment deposits. Underwater visual observations at location 4 have shown that the turbulent, sediment-laden lens of water resulting from sediment erosion, the nepheloid layer of Moore (1977), is 1–2 m thick and this compressed boundary layer may explain why sampling did not yield suspended material. At locations 5, 6, and 7 where a significant biomass of suspension feeders was present (Table 5), a nepheloid layer containing high concentrations of suspended particles was absent (scuba diving observations) and tidal currents here would not cause erosion (Table 8). Since suspension feeders must remain in contact with moving water above their habitat in order to feed, the erosion of the substrate represents a real threat to them. These considerations suggest that the impoverished community is limited by the dominant effect of tidal energy, either sediment instability or direct inhibitory effects on feeding by the suspension feeding animal, rather than by food supply limitations. Critical tidal current speeds above which suspension feeders experience growth impairment occur at about 25 cm/s for active pumping species such as mussels and other fouling organisms (Doochin and Smith 1951) and at 12 cm/s for the bay scallop *Argopecten irradians* (Kirby-Smith 1972).

The other key factor is the bulk concentration of seston, C, characteristic of each location and its relationship to C', the minimum concentration of seston required to maintain no overall changes in growth by a given population of suspension feeders. The interactions of both key factors are summarized in Fig. 4. Three possible concentration ranges for C need to be considered:

1. $C \gg C'$ where no mass transfer limitation occurs (line CD in Fig. 4). P is large and limited by other biological factors such as competition for space, direct inhibition of feeding above a maximum seston density (Schulte 1975) or direct inhibition by tidal velocities in excess of species-specific maxima.
2. $C' = 0.2$–$0.8C$, where turbulent mass transfer controls P. As N_A increases P increases to a maximum set either by the ability of tidal currents to erode the sediment (line AC) and hinder settlement or the species specific effect of faster currents on feeding ability. The lower limits for turbulent mass transfer are set by laminar flow conditions or where tidal currents are low (line BD).
3. $C' > C$ where seston concentrations are too low to support a population of suspension feeders (line AB, Fig. 4).

Unfortunately, we know of no empirical data for C' in terms of particulate ATP-seston observed seasonally and hence the analysis cannot be used to predict P from the known C values. Possibly the ration/growth

TABLE 7. Turbulent supply of seston to the sediment–water interface, N_A as in equation (4). V and C are means of 13 tidal observations, $\gamma = 0.003$ and $C^* = 0.5C$.

Location	Season	V m/s	C pg ATP/m³	N_A pg ATP·m⁻²·s⁻¹
1	Spring	.28	142	.06
	Summer	.36	1181	.64
2	Fall	.75	71	.08
	Winter	.22	69	.02
	Spring	.27	197	.08
	Summer	.27	1397	.57
3	Fall	.18	73	.02
	Spring	.05	344	.03
	Summer	.05	756	.06
4	Fall	.10	190	.03
	Winter	.09	145	.02
	Summer	.08	1238	.15
5	Fall	.38	412	.23
	Winter	.22	364	.12
	Spring	.10	349	.05
	Summer	.13	1487	.29
6	Spring	.16	69	.02
	Summer	.15	201	.05
7	Fall	.19	261	.07
	Winter	.22	74	.02
	Spring	.19	198	.06
	Summer	.15	193	.04

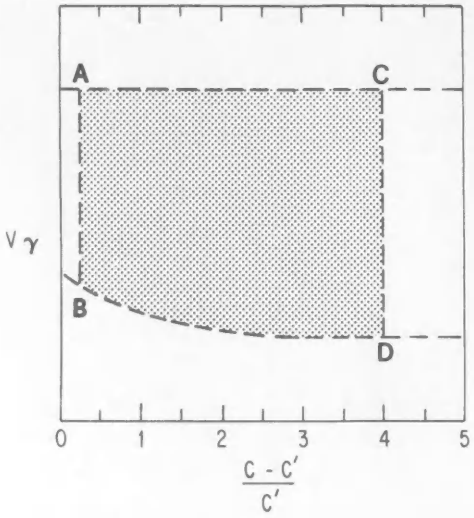

FIG. 4. Phase diagram showing the potential region for mass transfer limitation (stippled) for suspension feeding animals in different conditions of current speed times roughness (arbitrary scale) versus relative seston supply. Letters are explained in the text.

data for marine mussels of Bayne (1976), which are based on numbers of algal cells/L seawater, could be converted to ATP-seston concentrations, but is not attempted here.

An indicator of whether ATP-seston mass transfer limitation of population size and growth of suspension feeders may occur is provided by the dimensionless expression $P\gamma V/R\alpha$ which requires no knowledge of C' or C^*. If the dimensionless number lies between 4.00–0.25 equivalent to C–C'/C values when $C' = 0.2$–$0.8C$, mass transfer limitation is feasible. Based on observed P, mean V, setting $\gamma = 0.003$, $\alpha = 1.0$ and $R = 8.3 \times 10^{-4}$ to 4.15×10^{-3} m³/s, mass transfer limitation of the population is feasible at stations 3, 4, and 6. At stations 5 and 7, the higher values (10–20) for this expression indicate that $C \gg C'$ and that suspension feeders here are limited by factors other than mass transfer constraints.

The characteristics of the major macrofaunal communities are summarized in Table 9; the current velocities shown need further field and experimental investigation. Thus in reworked deposits containing mobile deposit feeders, as occurs at location 3, there is complete exclusion of suspension feeders. Whether this can be explained by the amensalism hypothesis (Rhoads and Young 1970) or the alternative of low mass transfer of seston suggested here can only be decided by further direct observation. It should be noted that the "biotic groups" of Rhoads and Young (1970) viz. *Suspension feeding*, *deposit feeding*, and *mixed* are defined differently from those in Table 9. Field observations by Sergerstråle (1973) show an inverse relationship between recruitment of *Macoma* (facultative suspension feeder) and *Pontoporeia* (deposit feeder) which was thought to be regulated by the amphipod eating the newly settled bivalve larvae. This apparent

TABLE 8. Observed tidal currents and critical erosion velocity calculated from data of Hjulström (in Perkins 1974). Data based on 26–52 observations at all seasons.

Location	Percentage of time > 25 cm/s	Critical erosion velocity for MDϕ cm/s	Percentage of time > critical erosion velocity
1	58	50 (35–65)	15
2	44	25 (20–35)	46
3	8	150 (75–230)	0
4	2	15 (12–22)	15
5	23	150 (70–220)	0
6	19	70 (55–130)	0
7	19	100 (65–190)	0

TABLE 9. Sediment–water interface parameters of macrofaunal communities.

Parameters	Community		
	Impoverished	Mixed	Deposit
Mean current velocity cm/s	>30	<30	<critical erosion velocity
Percentage of time > 25 cm/s	>30	<30	<30
Turbulent supply of seston	High or absent	Low to high	Low
Net deposit erosion	High	Low	Absent
Net sediment deposition	Absent	Low to high	High
Bioturbation	Absent	Absent or poorly developed	Present

support of the amensalism hypothesis may apply only where mixed communities are present in borderline hydrodynamic conditions and where it is possible that direct biotic interactions of this kind are more important.

Support for the mutual exclusion hypothesis (Wildish 1977) is provided by the ordering of the values N_A for each location which, apart from the two impoverished communities, correlate well with an independent assessment of the trophic types at each. Thus, N_A at location 5 (mixed community consisting mainly of suspension feeders) is five times greater than at 3 (deposit ingesting) during summer. For mixed communities where current speeds are intermediate and other factors variable (see Table 9) the presence together of both key groups, in contradiction of the amensalism hypothesis, may be due to the wider scope for activity of both groups in the intermediate physical conditions. This also provides a satisfactory explanation for the greater species diversity observed at mixed locations such as 4 (Table 4). Such evidence is not conclusive and further work is obviously necessary to test the trophic group mutual exclusion hypothesis. Of prime importance is the need to obtain actual values for C^* and C'. In the case of C' observations should be made with suspension feeders under controlled conditions to determine both the maintenance and optimum rations as measured by ATP-seston.

The results presented are a preliminary attempt to estimate growth potentials from the food available to suspension feeders. One difficulty with such a method is that the exact nature of the food is unknown; for instance, the degree to which suspension feeders are selective, the value of live or dead organic matter and dissolved organic molecules, and the role of symbiotic microflora within the gut are poorly known (see Jorgensen 1966; Banse 1974). All seston sizes greater than a few microns are filtered by the suspension feeders discussed by Jorgensen (1966) and hence the measurement of ATP as an approximate indicator of biomass for live microorganisms of unknown type seems a reasonable first approximation to the food quality of seston up to the optimum ration above which the growth rate declines. The use of other parameters such as organic carbon, chlorophyll, or protein content may prove to be better for this purpose. None of these methods would be able to distinguish food unsuitable for some other reason, such as the apparent effect of the anaerobic bacterium *Chromatium* sp. on pseudofaecal rejection by *Crassostrea* (Loosanoff 1949). A second difficulty is that suspension feeders need not, or are unable, to ingest all the seston filtered by them (see Widdows et al. 1979) and variable amounts are rejected as pseudo-faeces or by rapid passage in the gut.

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Energy Content Analysis from Weight and Liver Index Measurements of Immature Pollock (*Pollachius virens*)[1]

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JENSEN, A. J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachius virens*). J. Fish. Res. Board Can. 36: 1207–1213.

Variations in energy contents of liver and musculature of immature pollock (*Pollachius virens*) were analyzed by bomb calorimetry and then correlated to the liver index (liver weight as a percentage of body weight). For fish weighing between 400 and 1500 g, relationships between energy contents of liver and musculature and the liver index were described by mathematical functions. The mean energy content of other fish tissues, excluding liver, musculature, and gonads was constant. The total energy content of an immature pollock can thus be determined. The same relationships should be adaptable to other species that store their primary fat reserves in the liver.

Key words: *Pollachius virens*, liver index, energy content

JENSEN, A. J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachius virens*). J. Fish. Res. Board Can. 36: 1207–1213.

Nous avons analysé, à l'aide de la bombre calorimétique, les variations du contenu énergétique du foie et de la musculature de goberges (*Pollachius virens*) immatures et les avons ensuite reliées à l'indice hépatique (poids du foie en pourcentage du poids du corps). Chez des poissons pesant entre 400 et 1 500 g, les relations entre le contenu énergétique du foie et de la musculature et l'indice hépatique sont décrites par des fonctions mathématiques. Le contenu énergétique moyen des autres tissus, à l'exclusion du foie, de la musculature et des gonades, est constant. On peut donc déterminer de cette manière le contenu énergétique total d'une goberge immature. Les mêmes relations devraient pouvoir s'adapter aux autres espèces qui entreposent leurs réserves de graisse primaires dans le foie.

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A long range program (The "Havbiomodeller" project) was started in Norway to develop mathematical and numerical models of the physical, chemical, and biological processes in the ocean in order to be able to estimate past, present, and future states of the system. Balchen (1976) described a theoretical model of the energy storage and growth of fish. This model was compared with data from wild pollock (*Pollachius virens*), a lean fish which stores its primary energy reserves in the liver as fat.

Because the existing procedure for obtaining the total energy content of fish sampled at intervals was laborious to carry out, a simpler method for energy analyses was needed. Therefore, I looked for a relationship between the liver index (liver weight as a percentage of body weight) and the energy content of liver and musculature of immature pollock. An estimate of the total energy content of the fish could then be made from weight and liver index measurements. The equations developed should also be applicable to other fish species which store their energy reserves in the same way as pollock.

Materials and Methods

The pollock were taken by seine off the coast of Trøndelag, Norway. About 120 pollocks between 400 and 1500 g were examined. Gross body weight less contents of stomach and intestine was determined to within 1 g. A pollock of 1500 g could be mature, but no fish used in this study had their gonads developed. The largest fish from which data were used were caught in a bay in Trøndelag, Norway, where the connection to the sea had been closed for fish. The pollock belongs to a population of fish which was taken by seine off the coast of Trøndelag, tagged individually, then brought into the bay and observed for about 15 mo. We sampled at regular intervals, but mature fish were never found. The possibility that any fish had spawned at an earlier time was rather slight, hence we applied the term "immature" to all fish studied.

Tissue samples were oven dried at 105°C until a constant weight was reached. Then water content and dry matter fractions were determined. Lipids in the liver which were in a liquid state at 105°C, were defined as oil. Fractions of liver oil and dry matter were determined by weighing the liver before and after oil removal.

[1]Contribution to the "Havbiomodeller" ("Ocean-biomodelling") project, Norway.

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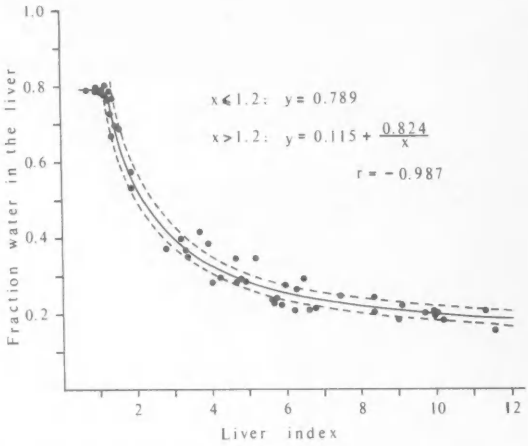

FIG. 1. Relationship between the relative weight of water in the liver and the liver index. 95% confidence limits for the regression curve are shown.

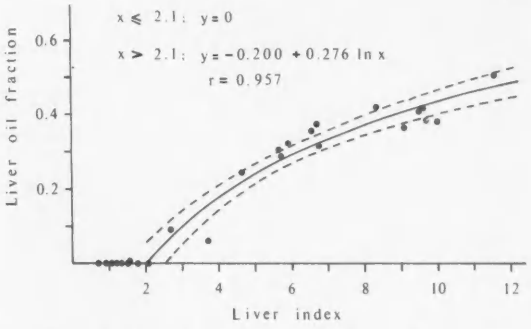

FIG. 2. Relationship between the relative weight of oil in the liver and the liver index. 95% confidence limits for the regression curve are shown.

Energy content in all materials was determined with a Phillipson microbomb calorimeter (Phillipson 1964). Two samples of 10–20 mg of each tissue were weighed on a Cahn electrobalance, type G, to within 10 μg before energy content was determined.

I combined data from three types of experiments to describe the energy content of pollock; growth experiments, storage experiments, and data from free living pollock.

I estimated the energy contents of liver and musculature tissues of pollocks with varying liver indexes. The mean energy content of other parts of the pollock fluctuates less with the condition of the fish than the energy contents of liver and musculature, as the primary energy reserves are stored mainly in liver and musculature (Bratland et al. 1976). I estimated the mean energy content of head, gills (with gill bones), musculature, bones not including the head and gill bones, skin, liver, gonads, other visceral tissues (after internal content removal), and body fluids of 10 wild fish by analysis of the dry matter and energy contents.

Liver index (liver condition) was determined as percent of wet weight of liver to wet body weight.

Curves were fitted to the data by the method of least squares.

Results

WATER, DRY MATTER, OIL, AND ENERGY CONTENT OF LIVER

The three components of the liver, i.e. water, dry matter, and oil, were separated by dehydration at 105°C. I found a clear inverse relationship between the water fraction of liver and the liver index (Fig. 1). However, when the liver index dropped beneath 1.2, liver lipid content was negligible and the fraction of water did not further increase. Liver indexes above 1.2 showed an inverse relationship between liver index and water content. An increase in liver index reflected storage of lipid in the liver. Lipid is not soluble in water, so the fraction of water drops with increased lipid volume. The lowest measured water content in liver was 15.2% in a pollock with a liver index of 11.56.

The relationship between the water fraction of the liver (w_L) and liver index (L) may be described as

(1a) $L \leq 1.2: w_L = 0.789$

(1b) $L > 1.2: w_L = 0.115 + \dfrac{0.824}{L}$

The liver oil fraction (o_L) increases with increasing liver index and for liver indexes below 2.1, oil content is negligible (Fig. 2). I found a rapid rise in oil content for liver indexes between 2.1 and 5.0, while a further increase in liver index caused only a slight increase in the liver oil fraction.

The following function was fitted to the data:

(2a) $L \leq 2.1: o_L = 0$

(2b) $L > 2.1: o_L = 0.276 \ln L - 0.200$

After water and oil were removed from the liver, dry matter remained.

By using (1) and (2), we determined the dry matter fraction (d_L) of the liver by

$$d_L = 1 - w_L - o_L$$

(3a) $L \leq 1.2 \quad : d_L = 0.211$

(3b) $1.2 < L \leq 2.1 : d_L = 0.885 - \dfrac{0.824}{L}$

(3c) $L > 2.1 \quad : d_L = 1.085 - \dfrac{0.824}{L} - 0.276 \ln L$

The dry matter fraction was about 0.211 when the liver index was less than 1.2. It increased to a maximum of 0.507 when the liver index was 3.0, followed by a nearly linear decrease, explained by an increasing fraction of fat stored as oil.

From these equations (1), (2), and (3) one can estimate the composition of water, dry matter, and oil in the liver when the liver index is known (Fig. 3).

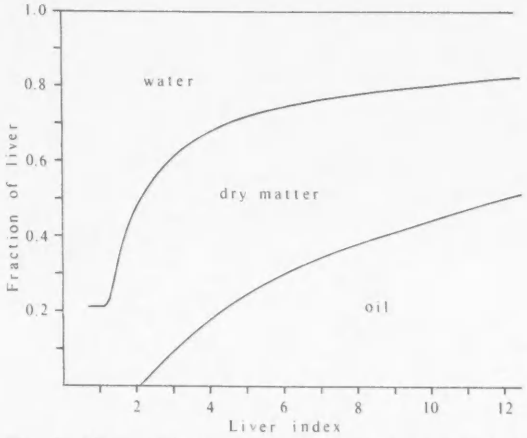

FIG. 3. The weight fractions of water, dry matter, and oil in the liver change with the liver index. When the liver index increases, the water fraction drops, and the oil fraction increases. The dry matter fraction reaches a maximum of 0.507 at a liver index of 3.0.

To calculate the energy content of the liver, one needs the data describing the energy contents of dry matter and oil. The liver oil of cod (*Gadus morhua*) contained mainly the fatty acids 16:0, 18:1, 20:5, and 22:6 (Jangaard et al. 1967a), and liver oil of pollock is assumed to have about the same composition, with an energy content (E_{Lo}) of 39.55 kJ/g (9.45 kcal/g). The amount of energy in liver dry matter (E_{Ld}) varies with its fat content, which in turn increases with an increasing liver index (Fig. 4). At high liver indexes, the energy content of the liver approaches the energy content of fat (39.55 kJ/g). This may be described as

$$E_{Ld} = 39.55 - 16.49\, e^{-0.235\, L} \quad (4)$$

We calculated the relationship between the liver index and the mean energy content of the liver (E_L) by using equations (1) through (4), (Fig. 5):

$$E_L = d_L \cdot E_{Ld} + o_L \cdot E_{Lo} \quad (5)$$

WATER AND ENERGY CONTENT OF MUSCULATURE

The water content of the musculature varies with the condition of the fish. When the liver index is lower than 4.0, the fat reserves are small (Fig. 5), and proteins in the musculature are, to a greater degree, utilized for respiration. The water content is nearly constant (79–80%) when the liver index is between 4.0 and 7.0, while it decreases with higher liver indexes (Fig. 6). The relationship between the water content of the musculature (w_M) and the liver index was found to be

$$w_M = 0.8303 - 0.0213 \ln L \quad (6)$$

Energy content of the musculature (on a dry weight basis), in weak or ill pollock, is observed to have a small variance (Fig. 7) with nearly no measurable in-

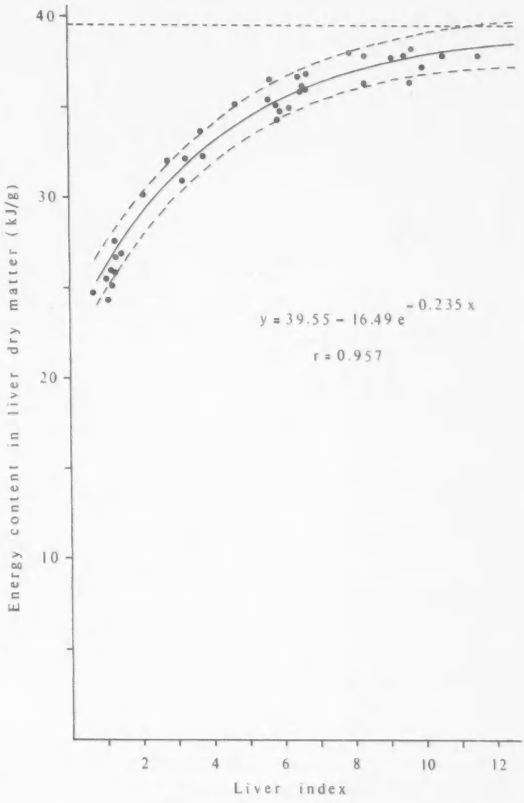

FIG. 4. Relationship between the energy content of dry matter in the liver and the liver index. 95% confidence limits for the regression curve are shown.

crease with increasing liver index. When the fraction of dry matter in musculature exceeded 0.21, corresponding to a liver index of about 7.0 (Fig. 6), we found an increasing energy content. The amount of energy in the musculature rose to values higher than for protein, and this is probably caused by an initial storage of fat in the musculature. The relationship between the fraction of dry matter in the musculature (d_M)

$$d_M = 1 - w_M \quad (7)$$

and its energy content on a dry weight basis (E_{Md}) may be formulated as

$$E_{Md} = 21.70 + 0.00046\, e^{37.85\, d_M} \quad (8)$$

By inserting eq. (7) into eq. (8), the energy content of musculature expressed by the liver index is

$$E_{Md} = 21.70 + 0.283\, L^{0.806} \quad (9)$$

Information from the energy content of musculature on a wet weight basis (E_M) would be even more useful to estimate active energy supplies. This is found by

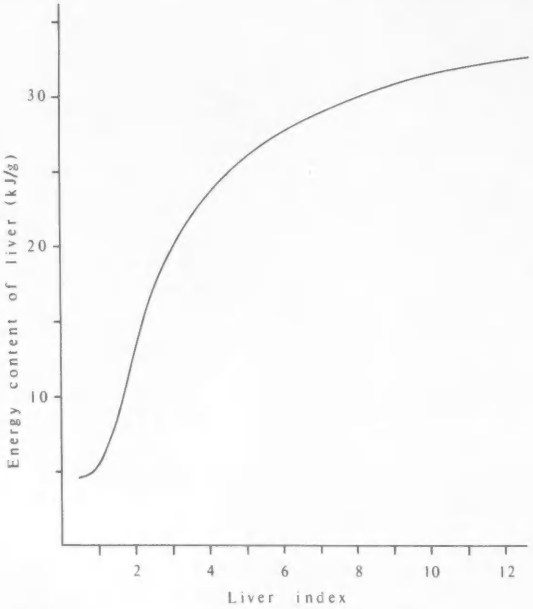

FIG. 5. Relationship between the liver index and the mean energy content of the liver (kJ/g wet weight) as calculated using equation (5) in the text.

multiplying eq. (9) with eq. (7), (Fig. 8)

(10) $E_M = d_M \cdot E_{Md}$

Knowledge about the amount of musculature in pollock under various conditions makes it possible to calculate the total amount of energy stored in musculature. We determined this by removing the musculature from 90 fish, weighing, and calculated the fraction of musculature to body weight. This method was inaccurate, however, and there was a large variation in muscle volume from fish to fish with similar physical characteristics (Fig. 9) but a trend was found. We observed a distinct change in muscle volume when the liver of starving fish decreased to beneath 1.5% of the body weight. Liver fat content was negligible at this point, and the energy necessary for respiration had to be metabolized from proteins in the musculature. From the measurements, however, we did not find any distinct difference in the fraction of musculature between starving and growing fish, but the reason for this may be inaccuracies in the method used. When the liver index exceeded 1.5, the fraction of musculature decreased, but to a lesser degree than the relative increase of the liver. As a result the fish became fatter with increased liver index.

We have described the relationship between the liver index and the fraction of musculature (m) by two regression lines (Fig. 9).

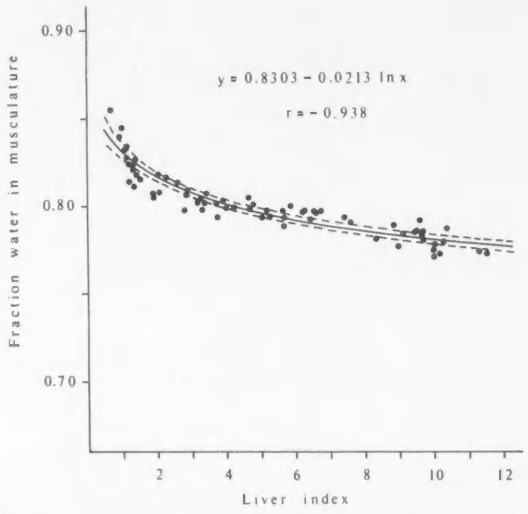

FIG. 6. Relationship between the relative weight of water in the musculature and the liver index. 95% confidence limits for the regression curve are shown.

(11a) $L < 1.5$: $m = 0.1207 + 0.2733\,L$

(11b) $L > 1.5$: $m = 0.5286 - 0.040\,L$

From Fig. 9 the relationship between the liver index and the fraction of musculature appears to be cyclic, but the method used to measure the fraction of musculature to body weight was too inaccurate to lay stress on this.

ENERGY CONTENT OF OTHER ORGANS AND THE WHOLE FISH

The fish were sexually immature. Analysis of gonads in 38 pollocks have shown that only 0.3% of the measured body weight was due to the gonads, whose mean water content was 88.7%. Hence, the energy stored in the gonads was neglected.

Earlier investigations on pollock have shown that when held alive without food for long periods, the liver was the primary energy resource. When the liver index decreased to beneath 4.0 the depletion of white muscular tissue increased (Bratland et al. 1976). As the liver fat and white musculature proteins are the primary energy reserves in pollock, the other parts of the body, except in extreme situations, have a more constant energy content. To estimate a mean energy content of the rest of the fish, when liver and musculature are excluded, we analyzed 10 pollocks, and found a mean energy content (E_R) of 3.34 kJ/g wet weight for these tissues (Table 1).

The relations worked out in this study make it possible to estimate the total amount of energy (E) in an immature pollock given the weight and liver index. By

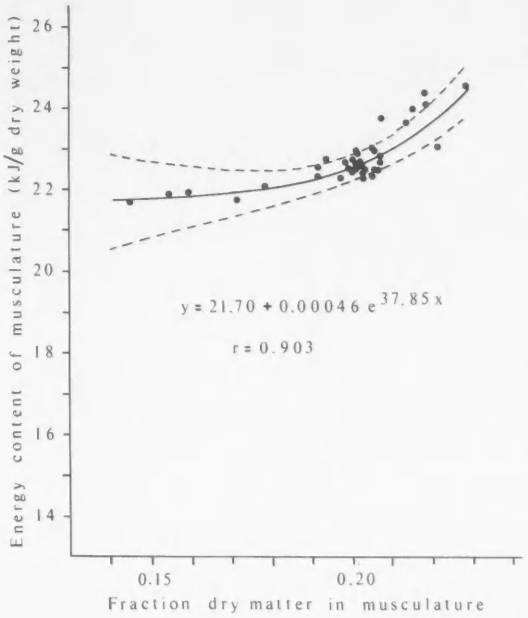

FIG. 7. Relationship between the dry matter fraction and the energy content of the musculature. 95% confidence limits for the regression curve are shown.

summing the energy contents of liver, musculature, and other parts of the fish, total energy is computed by

$$E = E_L \cdot W_L + E_M \cdot W_M + E_R \cdot W_R$$

$$(12) \quad E = (0.01L \cdot E_L + m \cdot E_M + (1 - 0.01L - m) \cdot E_R) \cdot W$$

E_L is energy content of liver, E_M is energy content of musculature, E_R is energy content of the parts of the fish other than liver and musculature, W_L is weight of liver, W_M is weight of musculature, W_R is weight of the fish other than liver and musculature, L is the liver index, m is fraction of musculature to body weight, and W is total weight of the fish.

Discussion

The utilization of the liver index as a measure of the condition of a fish is useful only for fishes which store their fat reserves in the liver, i.e. Gadidae, sharks and rays (Shul'man 1974). This method has been used by Graham (1923) and Jangaard et al. (1967b) for cod, and Bratland et al. (1976) for pollock. Heidinger and Crawford (1977) subtracted the gonadic weight from gross body weight before calculating the index, and called it "Liver-somatic Index". As our pollock were immature, the liver index, as used in this paper, covers both Graham's "Liver Condition" and Heidinger and Crawford's "Liver-somatic Index."

The very good correlations between liver index and

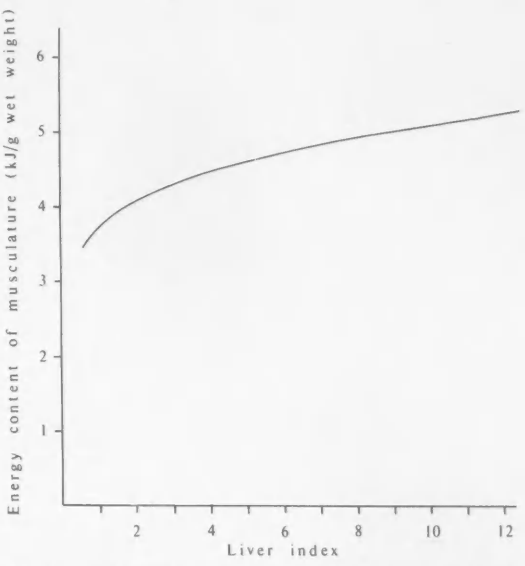

FIG. 8. Relationship between the liver index and the energy content of the musculature (kJ/g wet weight) as calculated using equation (10) in the text.

content of water (Fig. 1) and oil (Fig. 2) in the liver, and the energy content of dry matter (Fig. 4), confirmed that the liver index was an excellent measure of the condition of the pollock.

The relationship between liver index and dry matter and the energy content of musculature are not quite as evident as that found between the liver index and oil, dry matter and energy content of the liver. These

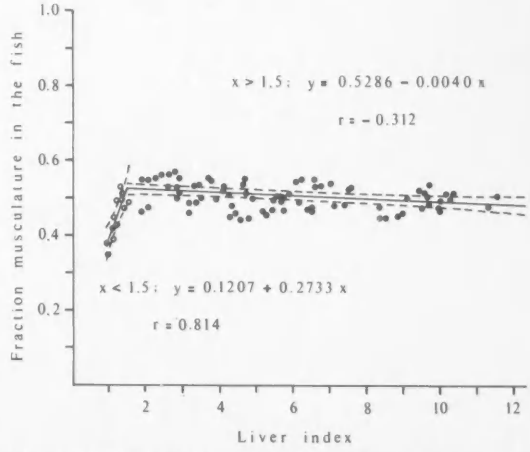

FIG. 9. Relationship between the relative weight of musculature in pollock and the liver index. 95% confidence limits for the regression lines are shown.

TABLE 1. Distribution of pollock tissues (percent of total fish by weight) with water and energy storage (± 95% confidence intervals). Average weight of fish 629 ± 133 g.

Part of the fish	Number	Percent of the fish wet weight	Water content (%)	Energy (kJ/g wet weight)
Musculature	10	49.91±1.54		
Skin	10	9.36±0.48	70.09±4.20	5.04±0.70
Bones	10	9.90±1.04	72.77±2.11	2.90±0.25
Head	10	13.24±0.47	80.11±1.21	3.24±0.52
Gills	10	2.94±0.14	76.45±1.92	4.17±0.37
Liver	10	4.62±1.13		
Gonads	38	0.30±0.03	88.72±1.34	3.08±0.34
Other vicera	10	3.93±0.44	75.80±1.24	5.12±0.32
Body fluids	10	5.85±0.86		

TABLE 2. Energy content of musculature in pollock (kJ/g wet weight) comparing experiments by Bratland et al. (1976) and the regression eq. (10) developed in this study.

Locality	Sample time (d)	Liver index	Energy content of musculature	
			Bratland et al.	Regression eq. (10)
Leines	70	2.36	4.20	4.18
Sørøy	60	8.31	4.99	4.99
Lepsøy	49	6.58	4.79	4.82
Laboratory exp. I	35	3.22	4.59	4.36
Laboratory exp. II	42	5.11	4.59	4.65

variations in dry matter and energy content of musculature are not as pronounced as that for the liver, however. Hence, a possible weakness in the connection between liver index and quality of the musculature would make a rather small error in the estimation of energy content of the musculature (Fig. 8).

Bratland et al. (1976) analyzed the contents of water, protein, lipids, carbohydrates, and ash in the white musculature of pollock in five experiments where pollock were starved and observed for 2–4 mo. The energy content of musculature in their experiments could be calculated by using data midway in each experiment. I compared these results with those calculated by using the developed energy equation with the corresponding liver index and found a favorable comparison (Table 2).

The mean energy content of pollock increased from 3.94 kJ/g to 6.27 kJ/g as the liver index increased from 2.0 to 8.0. This was caused by a slight increase in energy storage of musculature, but primarily by increasing storage of fat in the liver.

The annual variation in liver index of immature pollock in a bay in Trøndelag, Norway, changed from a minimum of 3.5 in June to a maximum of 5.9 in November, which reflected a variation in energy content from 4.54 to 5.48 kJ/g (A. J. Jensen unpublished data). This is consistent with energy content found in other fish species. Mann et al. (1972) reported seasonal changes in energy content from 3.56 to 4.82 kJ/g for roach (*Rutilus rutilus*) and 3.65–6.08 kJ/g for bleak (*Alburnus alburnus*). MacKinnon (1972) found a range of 3.45–5.05 kJ/g and 3.91–5.16 kJ/g for females and males, respectively, throughout the year for American plaice (*Hippoglossoides platessoides*).

The method developed in this paper appears to estimate satisfactorily the energy content of liver, musculature, and the whole fish. It should be useful to fish species which store their primary fat reserves in the liver, i.e. Gadidae, sharks, and rays.

Acknowledgments

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Morphological and Ecological Divergence Within the Lake Whitefish (*Coregonus clupeaformis*) Species Complex in Yukon Territory[1]

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BODALY, R. A. 1979. Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon Territory. J. Fish. Res. Board Can. 36: 1214–1222.

Two forms of lake whitefish (*Coregonus clupeaformis* species complex sensu McPhail and Lindsey [1970]) were found in each of five lakes in Yukon Territory. They are characterized by differences in gill raker counts. Low gill raker fish are benthic feeders and are found almost exclusively near the bottom while high raker fish are largely plankton feeders, being found throughout the lake water column. High raker fish have longer and more closely spaced gill rakers than low raker fish. They also have shorter life spans and mature earlier than low raker fish. Lakes supporting these sympatric populations of lake whitefish have no cisco populations. The low gill raker member of these sympatric populations seems to be equivalent to most other Yukon lake whitefish whereas the high raker member appears to be the unusual member of each sympatric pair.

Key words: whitefish, lake, feeding, morphology, growth, divergence, Yukon Territory, sympatric populations

BODALY, R. A. 1979. Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) species complex in Yukon Territory. J. Fish. Res. Board Can. 36: 1214–1222.

Nous avons trouvé dans chacun de cinq lacs du Territoire du Yukon deux formes de grand corégone (complexe *Coregonus clupeaformis* sensu McPhail et Lindsey [1970]). Elles sont caractérisées par des différences dans le nombre de branchicténies. Les poissons à nombre moindre de branchicténies se nourrissent de benthos et se rencontrent presque exclusivement près du fond, alors que les poissons à nombre élevé de branchicténies sont en grande partie des planctophages et se trouvent dans toute la colonne d'eau du lac. Les branchicténies, chez les poissons à nombre élevé, sont plus longues et plus rapprochées que celles des autres poissons. En outre, les poissons à nombre élevé ont une durée de vie plus courte et atteignent la maturité sexuelle plus tôt que les poissons à nombre moindre de branchicténies. Les lacs qui supportent ces populations sympatriques de grands corégones sont dépourvus de populations de ciscos. Les membres à nombre moindre de branchicténies semblent être l'équivalent de la plupart des grands corégones des autres lacs du Yukon, alors que les membres à nombre élevé semblent être l'élément exceptionnel de chaque paire sympatrique.

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WHITEFISH (Coregonidae) have undergone extensive recent speciation throughout their range. Situations of the sympatric coexistence of distinct forms are known throughout the Old World (Berg 1948; Svardson 1957) and, less commonly, in North America (Kennedy 1943; Lindsey 1963; Fenderson 1964). Previous studies of these closely related sympatric whitefish have provided information on the extent of divergence which has taken place, as well as the form and effectiveness of isolating mechanisms.

The present study concerns situations of sympatric lake whitefish (*Coregonus clupeaformis* species complex sensu McPhail and Lindsey [1970]) in the Yukon Territory. Lindsey (1963) presented evidence that sympatric lake whitefish populations, characterized by high and low modal gill raker counts, are present in Squanga Lake, Yukon Territory. These populations differed in feeding and in depth distribution and spawned separately (Lindsey 1963). This paper documents, first, the presently known distribution of sympatric lake whitefish populations in the Yukon Territory, and second, the extent of morphological and ecological divergence which has occurred between these sympatric populations.

[1]Based on a thesis submitted in partial fulfillment of the requirements for the degree of Ph.D. from the University of Manitoba, Winnipeg, Man.

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Materials and Methods

COLLECTION OF SPECIMENS

Eighty-nine lakes in the Yukon Territory and adjacent

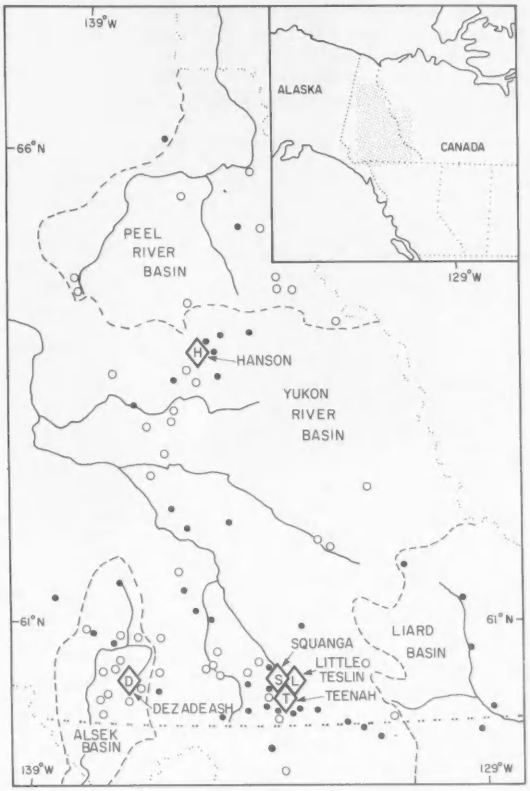

FIG. 1. Locations of lakes in Yukon Territory and adjacent areas which have been sampled for fish. Open circles: no lake whitefish caught. Closed circles: one form of lake whitefish caught. Diamonds: two sympatric forms of lake whitefish.

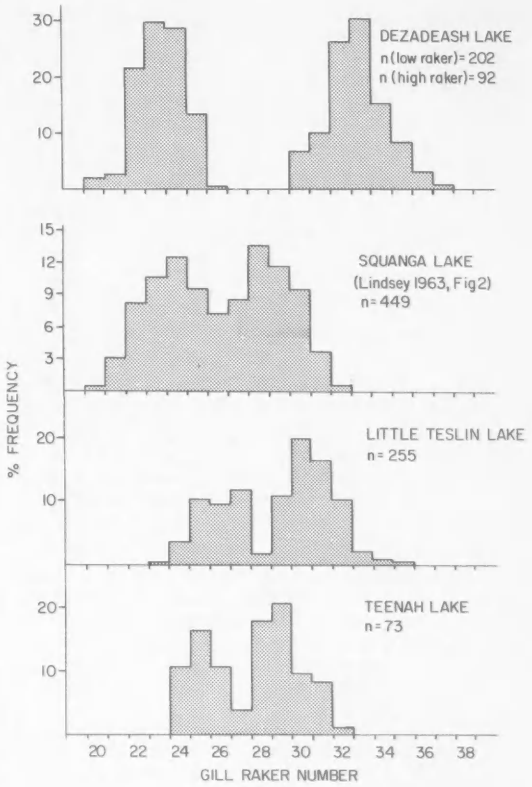

FIG. 2. Gill raker counts for lake whitefish from Little Teslin, Teenah, Squanga (field counts, from Lindsey 1963), and Dezadeash lakes.

areas in northern British Columbia, in the drainage basins of the Yukon, Alsek, Upper Liard, and Peel rivers were fished by gill net between 1968 and 1975 (Fig. 1). Experimental gill nets (length 38.1 m, depth 2.1 m, with panels, in order, of 25, 51, 76, 38, and 64-mm stretched mesh monofilament nylon) were generally set in the evening and raised the next morning. All parts of the water column, including shallow inshore areas and bottom and surface offshore areas were sampled. Fish were frozen soon after capture, shipped to the laboratory and stored frozen for varying periods before examination. In addition, a formalin preserved collection of small lake whitefish from Hanson Lake, Y.T. (Collection BC60-673), was examined at the University of British Columbia fish museum. The naturally occurring fish fauna of Hanson Lake was exterminated in 1963 for the purpose of planting rainbow trout (Walker et al. 1973). Only northern pike (*Esox lucius*) are found in the lake at present.

MORPHOLOGICAL MEASUREMENTS

Gill rakers were counted under a dissecting microscope by cutting forward to the symphysis and folding back the gill cover of larger fish, and after removal of the first gill arch of smaller fish. Counts were recorded as upper gill raker numbers (not including the "middle" gill raker at the intersection of the upper and lower gill arches) and lower gill raker number (including the "middle" raker). Fork length was measured to the nearest millimetre. Total (both sides) gonad volume was measured by water displacement to the nearest 0.1 mL. Additional morphometric and meristic measurements were made following Lindsey (1963): prepostorbital distance, head length, pectoral origin, pectoral length, pelvic origin, and body length (fork length minus head length). The following meristic counts and morphometric measurements followed Lindsey (1962): gill raker length, head depth, peduncle depth, interorbital width, maxilla length, maxilla width, adipose fin length, suprapelvic scale count, peduncle scale count, and dorsal fin ray count. Lateral line and above lateral line scale counts were made following Hubbs and Lagler (1958) and gill raker space was measured following Kliewer (1970). Calipers were used for the following morphometric measurements: length of lower arch (distance from middle of the base of the gill raker at the intersection of upper and lower first gill arch to middle of base of the gill raker

TABLE 1. Relative size (or number) of 24 morphological characters for high raker lake whitefish as compared to the size (or number) for low raker lake whitefish from Dezadeash, Little Teslin, Teenah, and Squanga lakes. Squanga results from Lindsey (1963) and Lindsey (unpublished data). Morphometric characters tested by analysis of covariance and meristic characters by χ^2 contingency tables. Greater, Less: significant difference at $P < 0.05$. —: no significant difference. Blank: not tested.

Morphological character	Dezadeash	Little Teslin	Teenah	Squanga
Gill raker length	Greater	Greater	—	Greater
Gill raker space	Less			Less
Average gill raker space	Less	Less	Less	
Length of lower gill arch	Less	Less	Less	
Premaxilla height	Less	—	—	
Maxilla length	—	—	Less	—
Maxilla width	—	—	—	
Prepostorbital distance	Less	Greater	Less	Less
Interorbital width	Less	Greater	—	Greater
Vertical pupil diameter	Less[a]	Greater[c]		
Horizontal pupil diameter	—	Greater[c]		
Eye diameter	Less	Greater[c]	Less	Less
Head depth	Less	—	Less	Less
Head length	Less	—	Less	Less
Pectoral origin	Less	—	Less	Less
Pectoral fin length	—	—	Less	Less
Pelvic fin origin	Less	—	—	Less
Peduncle depth	—[b]	—	Less	—
Adipose fin length	Greater	—	—	—
Lateral line scale number	—	—		
Suprapelvic scales	—	—		
Above lateral line scales	—	--		
Peduncle scales	Less	—		
Dorsal fin ray count	—	—		

[a]Less for fish below 150 mm body length; larger fish similar.
[b]Less for fish below 125 mm body length; Greater for fish above 125 mm body length.
[c]Greater for fish above 150 mm body length only.

farthest along the lower arch), average gill raker space (length of lower arch divided by lower gill raker number), vertical pupil diameter (diameter of pupil of eye in vertical dimension), horizontal pupil diameter (similar), eye diameter (horizontal diameter of exposed eye ball), premaxilla height (measured by placing one caliper jaw in the upper snout notch just behind premaxilla and measuring to the ventral edge of the premaxilla).

STATISTICAL TREATMENT OF MORPHOLOGICAL DATA

Fish were tentatively placed in high or low gill raker groups on the basis of gill raker counts (Fig. 2) and gonad volume (Fig. 4). Analysis of covariance was used to discern morphometric differences between fish of these two groups. Fork length (in the case of gill arch measurements) or body length (fork minus head length) (in the case of body measurements) were the independent variables used. All morphometric variables were $\log_{10}$ transformed. Differences in the distributions of meristic counts between high and low raker fish from Dezadeash and Little Teslin Lakes were tested by $2 \times k$ contingency tables. Meristic data from Teenah Lake were not tested because of small sample sizes.

Stepwise discriminant analysis (Biomedical Computer Programs, U.C.L.A.) was carried out to determine the degree of morphological separation between high and low raker fish from the same lake and to attempt to assign all fish to one of the two groups. The residuals from the "pooled within" regression line (terminology from Thorpe (1976)) from the analysis of covariance were used as the morphometric variables. Discriminant analysis was first performed by including all morphometric (except gonad volume) and meristic variables, using as initial group assignments those made for analysis of covariance. Discriminant scores for fish for which a tentative group assignment could not be made were calculated from the discriminant function set up with fish which could be assigned to groups. Discriminant analysis was then performed again after deletion of upper and lower gill raker number and all other variables found to show significant correlation with total gill raker number on a within group basis.

STOMACH CONTENT ANALYSIS

Organisms found in stomachs were placed into major taxonomic groups and the percent volume contribution of each group was estimated by eye with the contents of each stomach spread on a petri dish. Taxonomic groups were then categorized as being either almost exclusively benthic or partially or totally pelagic following Kliewer (1970). A further category was made of crustacean plankton consisting of cladocerans, copepods and ostracods. Raw data from Squanga Lake was reexamined for presentation consistent with the present study.

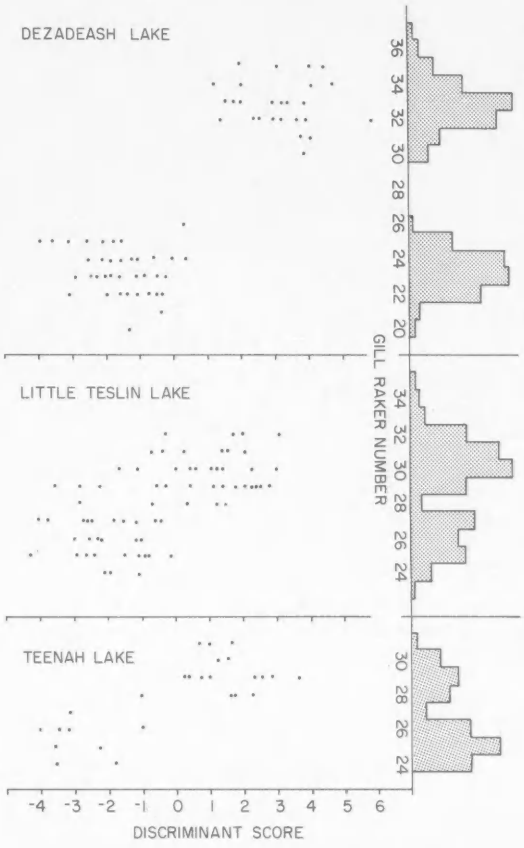

FIG. 3. Discriminant scores based on morphology (excluding gonad volume and gill raker number and other variables correlated on a within group basis with gill raker number) versus gill raker number. Discriminant functions are as follows: Dezadeash: discriminant score = −29.37 × (head depth) + 14.04 × (peduncle depth) −7.46 × (premaxilla height) + 26.32 × (gill raker length) −0.27. Little Teslin: discriminant score = −19.00 × (pectoral fin length) + 31.86 × (eye diameter) −14.41 × (maxilla length) + 22.11 × (gill raker length) −0.31. Teenah: discriminant score = 12.88 × (gill raker length) −64.73 × (length of lower arch) + 0.01.

AGE DETERMINATION

Fish were aged from scales taken from between the dorsal fin and the lateral line. Ages derived from scales were adjusted according to length/frequency plots because such plots showed that most scales failed to show the first annulus.

Results

MORPHOLOGICAL DIFFERENCES

Gill raker distributions were found to be bimodal for lake whitefish from Dezadeash, Little Teslin, and Teenah lakes, but only for the Dezadeash Lake sample were the two parts of the distribution completely separated (Fig. 2; Squanga Lake population gill raker distribution [field counts] from Lindsey [1963] shown for comparison). Fish from Hanson Lake (all specimens were less than 55 mm fork length) also showed a bimodal distribution in gill raker number, with modes at 21 and 29 gill rakers:

No. gill rakers	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Frequency	1	2	4	0	2	0	0	0	0	2	7	1	0	1

These sample modes are probably somewhat lower than the true values because small gill rakers can be overlooked in very small fish.

In all pairs of populations high raker fish had longer, closer spaced gill rakers and shorter lower gill arches, than had low raker fish (Table 1) with the exception of gill raker length comparisons for fish from Teenah Lake. Differences in characters not associated with the gill raker apparatus were not consistent between high and low raker fish from all lakes, but tended to occur in sets between high and low raker fish from a particular lake. Thus, relative to low raker fish, high raker fish from three lakes, Dezadeash, Teenah, and Squanga, had smaller heads (shorter prepostorbital distance, smaller interorbital width, shorter head length), smaller eyes, shorter fin origins and shorter fins (Table 1). In contrast, in Little Teslin Lake high raker fish were characterized by significantly greater prepostorbital distance, larger interorbital width and larger eyes than low raker fish.

The distribution of discriminant scores calculated with all morphological and meristic variables measured (except gonad volume) was bimodal for fish from Dezadeash, Little Teslin, and Teenah lakes, with no overlap between the two groups of fish found in each of these lakes. No significant differences between the discriminant scores for male and female fish were found for high or lower raker fish from any lake and sexes were therefore considered together.

Discriminant scores calculated without gill raker number or any morphological variable correlated, on a within group basis, with gill raker number, are plotted against gill raker number in Fig. 3. Although the extent of the separation of high and low gill raker fish varies from lake to lake, there is confirmation that the fish from all lakes can be placed in two distinct morphological groups; low gill raker fish tend to have a low discriminant score and high gill raker fish a high discriminant score (Fig. 3).

High raker fish from Dezadeash and Little Teslin lakes showed larger gonad volumes relative to fork length than did low raker fish (Fig. 4). This difference was noted for both sexes at almost all sample times for fish from Dezadeash and Little Teslin lakes (Fig. 4), Teenah Lake (not shown), and Squanga Lake (Lindsey 1963). Thus, despite the considerably smaller average size of high raker fish, absolute gonad volumes of

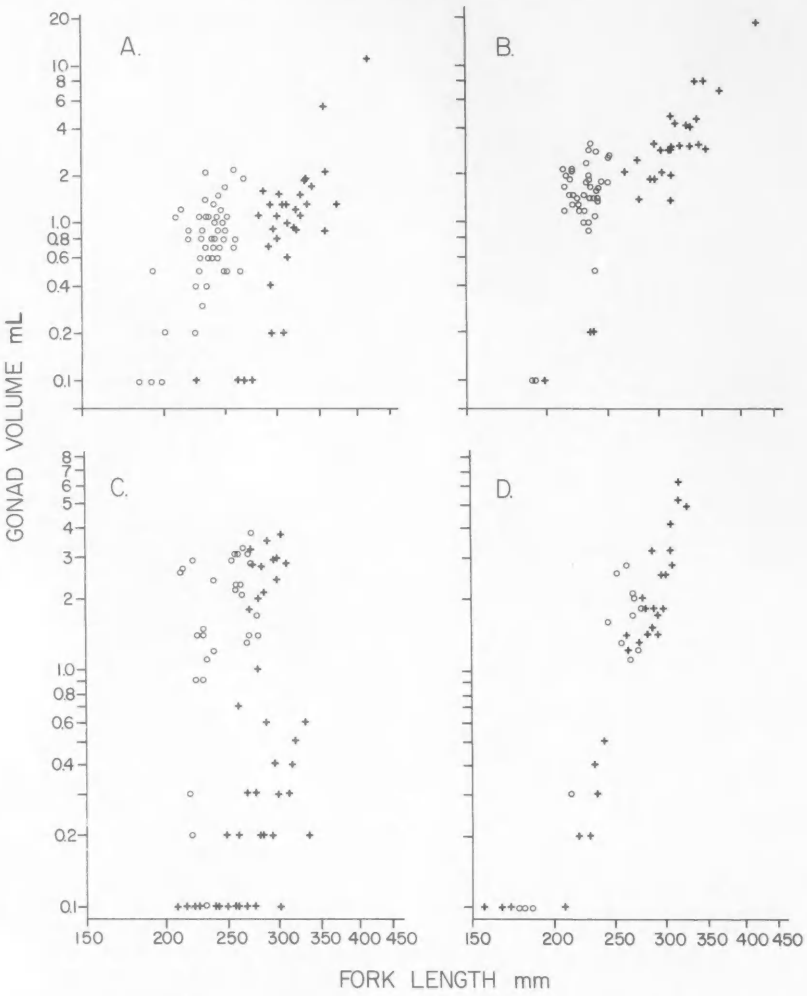

FIG. 4. Plots of gonad volume versus fork length for male and female high and low raker lake whitefish. Open circles = high raker fish, crosses = low raker fish. A. Males, Little Teslin Lake; B. Females, Little Teslin Lake (fish captured June 26–27, 1975); C. Males, Dezadeash Lake (fish captured August 22–26, 1973); D. Females, Dezadeash Lake (fish captured June 26–July 2, 1974).

mature fish were similar for high and low raker fish from all four lakes.

Growth of high and low raker fish from Little Teslin and Dezadeash lakes was similar during the first 5–6 yr of life (Fig. 5), although the average size of low raker fish caught in experimental gill nets always exceeded the average size of high raker fish. Lindsey (1963) did not age fish from Squanga Lake, but noted that low raker fish were on average larger than high raker fish. Growth of high raker fish appears to slow as these fish approach the maximum age captured in Little Teslin Lake (Fig. 5).

High raker fish mature earlier than low raker fish. For example, male high raker fish from Little Teslin Lake had mature testes at approximately 220 mm fork length (Fig. 4a), corresponding to fish of age 4+ (Fig. 5) while male low raker fish from the same lake show mature testes at approximately 290 mm fork length (Fig. 4b), corresponding to fish of age 6+ (Fig. 5).

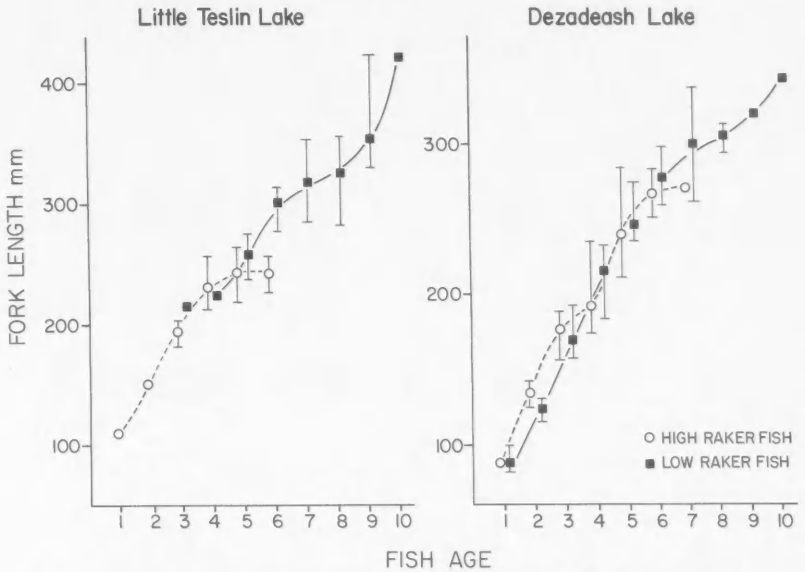

FIG. 5. Average size at midsummer versus age for high and low raker lake whitefish. High raker fish: filled squares. Ranges shown for samples of three or more fish. Curves fitted by eye. Little Teslin Lake fish captured June 26–27, 1975. Dezadeash Lake fish captured June 26–July 2, 1974.

ECOLOGICAL DIFFERENCES

In Dezadeash, Little Teslin, and Teenah lakes, nets set on the surface over deep water caught almost exclusively high raker fish (Fig. 6). Nets set on the bottom, either in deep or shallow areas, caught predominantly low raker fish. Differences in the spatial distribution of high and low raker fish were pronounced even in Dezadeash Lake, where the deeper areas fished were only 4.2 m deep and therefore the two 2.1-m deep gill nets effectively fished the entire water column. An exception to this pattern occurred in Teenah Lake where only high raker fish were caught near the bottom in deep water. Catches of high raker fish in Little Teslin and Dezadeash lakes were greater in surface nets (in deep or shallow water) during the night than catches during the day.

In all lakes studied, high raker fish were found to take mostly pelagic food composed mainly of crustacean plankton (Fig. 7). In contrast, low raker fish of large size in all populations examined were found to take mostly benthic food (Fig. 7). Only in Dezadeash Lake were sufficient low raker fish of small size taken to establish a feeding pattern, and these fish took mostly pelagic food (Fig. 7). The proportion of crustacean plankton eaten by these fish is similar to that of high raker fish from the same lake.

Generally, the order of abundance of food items in the stomachs of high gill raker fish was cladocerans, copepods, and chironomid pupae. Chironomid larvae, gastropods, and pelecypods were generally the most important food items of low raker fish, although chironomid pupae were important in the diet of low raker fish from Little Teslin Lake. A tendency for greater utilization of benthic food by fish captured near the bottom was evident for high and low raker fish from Squanga Lake, small low raker fish from Dezadeash Lake, and low raker fish from Little Teslin Lake (Fig. 7).

Discussion

It was known that two distinct forms of lake whitefish occur in Squanga Lake, Yukon Territory (Lindsey 1963) and the present study shows that sympatric lake whitefish forms also occur in Dezadeash, Little Teslin, and Teenah lakes, and until recently, in Hanson Lake. The two forms in Squanga Lake are known to be separated at spawning (Lindsey 1963).

Significant ecological and morphological divergence has occurred between high and low raker Yukon lake whitefish. High raker fish feed mainly on crustacean plankton (Fig. 7) and are found throughout the water column (Fig. 6) (Lindsey 1963). These fish have longer gill rakers and smaller spaces between gill rakers than low raker fish not only because they have more gill rakers but also because they have shorter gill arches. These findings are in agreement with the known relationship in fishes, and particularly within the genus *Coregonus*, of more and longer gill rakers and feeding

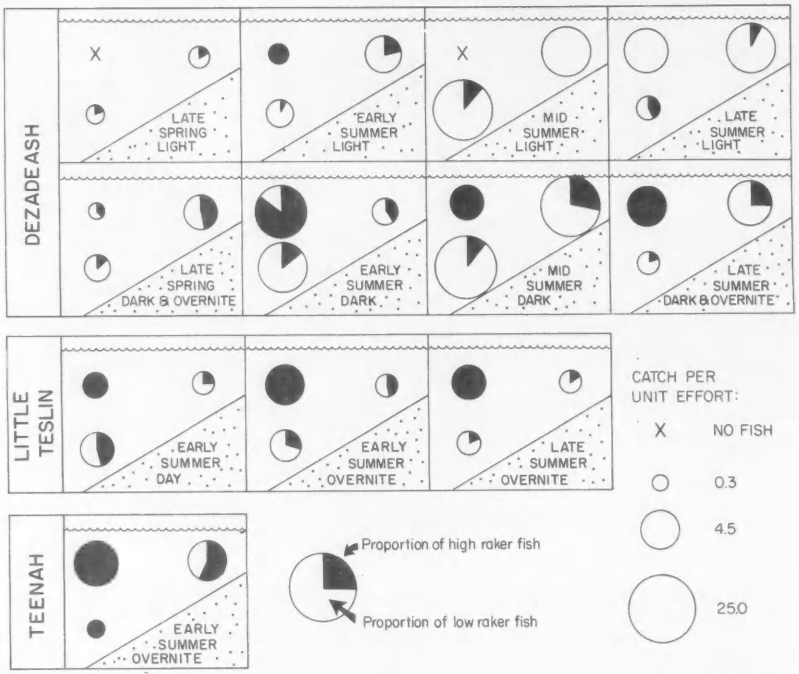

FIG. 6. Proportion of high and low raker lake whitefish and catch per unit effort in shallow (onshore) gill net catches and floating and bottom gill net catches in deeper water. One unit of fishing effort is one experimental gill net set for 1 h. Dezadeash Lake: shallow (2.1 m), deep (4.2 m); late spring June 6–15, 1974, early summer June 26–July 1, 1974, midsummer July 26–August 2, 1974, late summer August 10–26, 1973 and 1974. Little Teslin Lake: Shallow (2 m), deep (17 m); early summer June 26–27, 1975, late summer August 27–28, 1975. Teenah Lake: shallow (2 m), deep (18 m); early summer July 8–9, 1970.

on smaller, pelagic food particles (Svardson 1952, 1965; Scott and Crossman 1973; Kliewer 1970).

In contrast, low raker fish were usually caught near the lake bottom (Fig. 6) (Lindsey 1963) and larger fish of this form were found to be mainly benthic feeders. Low raker fish in Dezadeash Lake shifted from pelagic to benthic feeding in their fourth summer (Fig. 5 and 7) although Reckahn (1970) found that Lake Huron lake whitefish had largely completed this shift by the end of their first summer.

The high raker populations in Yukon lakes are distinctly shorter lived and earlier maturing than the low raker fish with which they are sympatric (Fig. 4 and 5). Such "dwarf" forms have been observed in other studies of sympatric whitefish populations (Fenderson 1964; Kennedy 1943; Svardson 1953).

Body proportion differences between the high and low raker populations of a particular lake tended to appear as sets of differences (i.e. smaller heads, eyes and fins) (Table 1) between parallel relative growth lines as was the case in studies where morphological differences were known to be the result of environmental and not genetic differences (Bodaly 1977; Martin 1949; Svardson 1950, 1951; Kliewer 1970). Also, these sets of relative growth differences between high and low raker fish were not consistent from lake to lake (Table 1) and thus were not always consistent with the known ecology of the fish. This evidence suggests that these relative growth differences are not the result of selection but rather may be due to environmental influences within individual lakes.

The low raker form of lake whitefish in Dezadeash, Little Teslin, Squanga, Teenah, and probably Hanson lakes appears to be equivalent to the ubiquitous form of the lake whitefish found throughout Yukon Territory. Gill raker modes and feeding patterns of low raker populations described in the present study are similar to most other Yukon populations (Lindsey et al. 1970; Clemens et al. 1968; Withler 1965). High raker lake whitefish appear to be the unusual members of the sympatric pairs in this study since gill raker modes and feeding patterns differ greatly from most other Yukon populations.

This high gill raker lake whitefish is a relatively rare

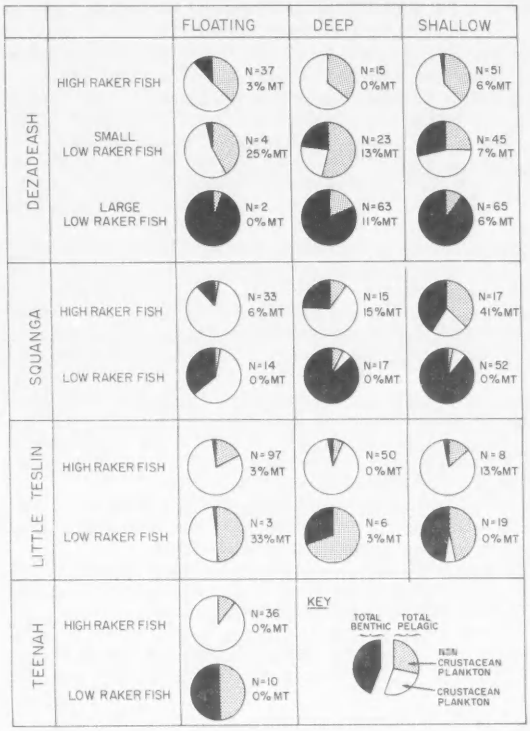

FIG. 7. Food of high and low raker fish classified according to place of capture (except Teenah Lake). Each pie diagram is divided to show relative percent volume contributions of benthic and pelagic food averaged over nonempty stomachs. Also shown is proportion of pelagic component which is crustacean plankton. Figures give number of stomachs examined and percent of stomachs empty. Dezadeash Lake fish captured June 6–15, June 26–July 2, July 26–August 2, 1974, and August 10–26, 1973 and 1974. Small low raker fish <200 mm fork length, large low raker fish ≥200 mm fork length. Squanga Lake fish captured June 1960. Little Teslin Lake fish captured June 26–27, and August 27–28, 1975. Teenah Lake fish captured July 8–9, 1970.

fish. At present only four lakes in Yukon Territory are known which support populations of these fish and the lakes themselves have some unique ecological features. First, although the least cisco (*Coregonus sardinella*) is common in Yukon Territory, lakes with high raker lake whitefish never have least cisco populations. The least cisco is probably able to exclude high raker lake whitefish due to competition for food. Both fish are planktivorous. Drainages in Maine which support the only other known sympatric lake whitefish pairs (Fenderson 1964) also lack any form of cisco. Similarly, dwarf, planktivorous whitefish populations are virtually absent within the geographic range of ciscos in Sweden (Svardson 1977).

Another unique ecological feature of Yukon lakes which support high gill raker lake whitefish is their comparatively high lake whitefish standing crops (Bodaly 1977; Lindsey 1963). Contributory factors may be the relatively shallow average depth, which perhaps provides for suitable spawning conditions as well as food, and scarcity of piscivorous fish in these lakes. The lake trout (*Salvelinus namaycush*) is absent from Squanga, Little Teslin, and Teenah lakes. Furthermore, only sparse populations of lake trout, burbot (*Lota lota*), and northern pike are found in Dezadeash, Squanga, Little Teslin, and Teenah lakes.

These rare sympatric pairs of lake whitefish populations afford interesting and unique material for the study of evolutionary processes and they could also provide a source of genes for fish culture. Unfortunately, man has carelessly caused the extinction of many sympatric lake whitefish populations. Both forms in Hanson Lake were eradicated by poison in order to promote angling. In British Columbia the only known sympatric pair of lake whitefish populations (in Dragon Lake) were also exterminated prior to planting rainbow trout (Lindsey et al. 1970). The dwarf form in Opeongo Lake, Ontario, may have disappeared following the deliberate introduction of ciscos. Opeongo Lake supported the only known sympatric lake whitefish populations in Central Canada. Two of the Yukon lakes with surviving sympatric pairs, Squanga and Little Teslin, lie close to the proposed route of a natural gas pipeline. Environmental disturbances created by the construction of this proposed pipeline could threaten the continued existence of the unique fish stocks of these lakes.

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Seiche Excitation in Port San Juan, British Columbia

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LEMON, D. D., P. H. LEBLOND, AND T. R. OSBORN. 1979. Seiche excitation in Port San Juan, British Columbia. J. Fish. Res. Board Can. 36: 1223–1227.

Seiche motions observed in San Juan Harbour with a bottom-mounted pressure gauge have been Fourier-analyzed and interpreted in terms of a theoretical model of oscillations in a rectangular basin with an exponential depth profile. Two of the observed periods (at 14.6 and 38.5 min) are identified with resonances of the basin; two other significant low frequency peaks (at 21 and 55 min) do not coincide with resonant periods of the basin and must be due to strong external forcing. Higher frequency fluctuations (20–160 s) are attributed to swell and to its subharmonic interactions with edge waves.

Key words: water waves, seiches, mathematical model, Juan de Fuca Strait, British Columbia

LEMON, D. D., P. H. LEBLOND, AND T. R. OSBORN. 1979. Seiche excitation in Port San Juan, British Columbia. J. Fish. Res. Board Can. 36: 1223–1227.

Les variations de niveau d'eau (seiches) observées à l'aide d'un manomètre installé au fond de San Juan Harbour ont été soumises à l'analyse de Fourier et interprétées à l'aide d'un modèle théorique des oscillations d'un bassin rectangulaire dont le fond est conforme à une courbe exponentielle. Deux des périodes observées (à 14,6 et 38,5 min) ont été identifiées à des résonnaces d'un tel bassin; deux autres pics spectraux de basse fréquence (à 21 et 55 min) ne correspondent pas à des périodes de résonance et doivent être dûs à des forces de même période extérieures au bassin. Des fluctuations de plus haute fréquence (périodes de 20 à 160 s) sont attribuées à la houle et à ses interactions sous-harmoniques avec les ondes de frontière.

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PORT San Juan is a small bay (6.5 km long, 2 km wide) situated on the coast of Vancouver Island, near the opening of the strait of Juan de Fuca (Fig. 1). Evidence of seiche action in Port San Juan has long been available from sea level records taken by the Canadian Hydrographic Service at their tide gauge at Port Renfrew. Visual examination of such records suggests the presence of two distinct seiches with periods on the order of 15 and 35 min, respectively. Investigation of all sea level records at Port Renfrew for the year 1973 (the first year during which the gauge was operational, after malfunctioning for several years) revealed no correlation between the occurrence of seiches and the phase of the tide. Seiches were seen to occur at any phase of the tide, but many tidal cycles often went by without detectable seiche activity. There was also no clear correlation between seiches and storms. Since there is no meteorological station in the immediate vicinity of Port San Juan, evidence of storms has been taken from the width of the short wave noise on tide gauge traces. This method is of course subject to criticism in that it includes the effects of swell as well as that of locally generated waves. A broader study including simultaneous sea level measurements and meteorological monitoring at many points along the coast of Vancouver Island might uncover some relation between storms and seiche action in Port San Juan; such a study was beyond the means available to the experimenters. There is however a greater frequency of seiche action in the late fall, winter, and early spring than in the meteorologically calmer summer months. Seiche amplitudes vary widely; they are commonly of the order of 5 cm. The largest amplitude seen was 15 cm.

Partly because of the difficulty of working with the rough analog traces of the stilling-well tide gauge, and mostly because of our ignorance of its exact time-response, we could not use the tidal records as the basis of a more precise analysis of the seiche oscillations. Consequently, an original time-series of water levels was obtained with a more accurate instrument over a period of seiche activity. These measurements are described below and interpreted with the help of a theoretical model of the response of Port San Juan to excitation at its mouth.

Data Collection

A bottom-mounted pressure gauge using a vibrotron transducer was adapted to measure sea-level displacements in Port San Juan. Originally designed (Galloway 1975) as a shallow-water tide gauge, the instrument was modified

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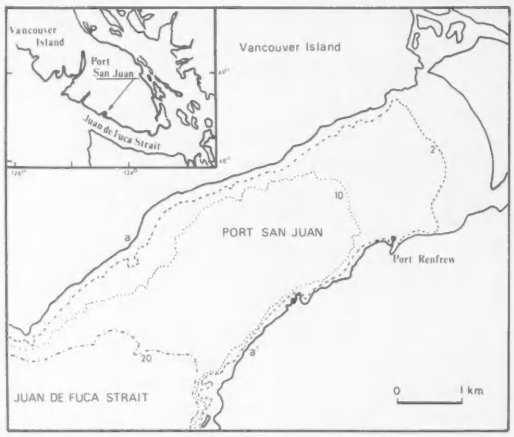

FIG. 1. Port San Juan and, in insert, its location on the west coast of Canada. Depth contours are labelled in metres.

to measure seiches. Data were recorded on several channels to give different combinations of resolution and sampling frequency. The maximum resolution available was 1.70 mm, measured every 21 s; the highest sampling rate was every 0.5 s, with a sensitivity of 3.23 mm. The system error was 30% of the sensitivity. Data recording was analogue, on magnetic tape. Further details of the design and operation of the instrument are to be found in Lemon (1975).

The data for the study were collected at Port Renfrew (Fig. 1) on February 26–28, 1974, near the permanent tide gauge. The sensor head was lowered to the bottom on a heavily weighted frame. There was 5.9 m of water over the sensor at high tide. The recorder was turned on at 0600 (PST), February 27, when seiches first appeared on the permanent tide gauge (used as a monitor). Reading continued, interrupted only by tape changes, every 6 h until 1915 on the same day.

Data Analysis

After calibration of the record (see Lemon 1975), the tide was removed from the data by subtracting the predicted tide at Port Renfrew from the observed sea level record. Substantial residual fluctuations of periods of many hours and amplitudes of up to 40 cm remained after removing the predicted tide. This residual trend was removed by fitting a smooth curve to it and subtracting the fitted curve from the signal. Three different curve-fitting methods were used: a polynomial fit to a low-passed version of the time series, a spline fit with error tolerance, and a combination of the two: a spline fit followed by a polynomial fit. The latter method gave a record (Fig. 2) whose spectrum had the least low-frequency energy (and was thus most completely detrended).

The power spectrum of the detrended series of Fig. 2 was calculated using a Fast Fourier Transform program (Froese 1970). The spectrum shown in Fig. 3 has been averaged over blocks of four Fourier coefficients. One of the main features of the spectrum is the deep gap in energy levels which occurs at periods of about 630 s (frequency $f = 1.6 \times 10^{-3} \cdot s^{-2}$, $\log f = -2.8$). At frequencies below the gap, five peaks are discernible. Three of these peaks are just significant at the 95% level; they occur at periods of 14.6 $\pm$ 0.6 min, 21 $\pm$ 1 min, and 55 $\pm$ 3 min. The other two peaks are just below the 95% level of significance and occur at 38.5 $\pm$ 2 min and 132 $\pm$ 4 min. The peaks at 38.5 (in spite of its lower significance) and 14.6 min compare fairly well with periods estimated from counting zero crossings on historical records of seiche activity measured by the per-

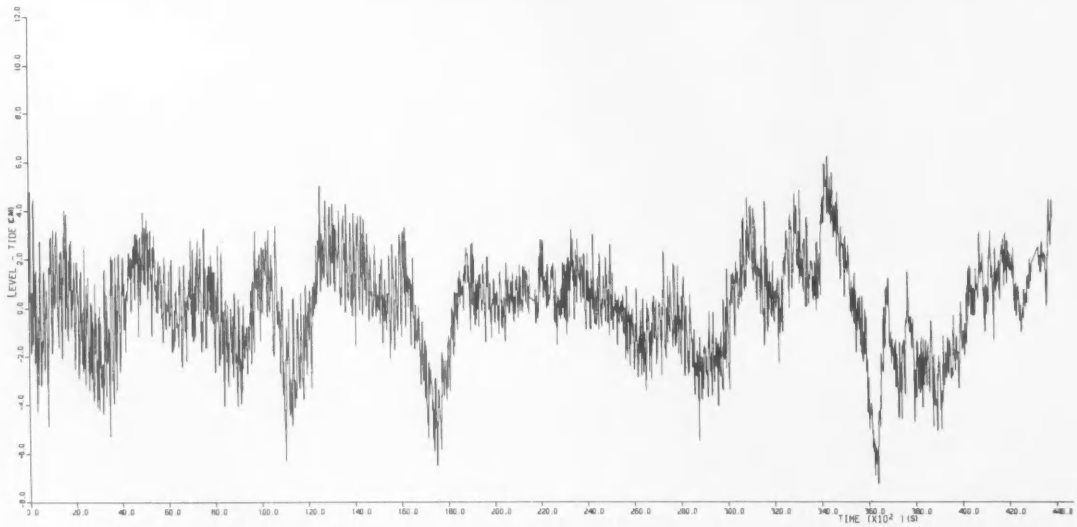

FIG. 2. Sea-level variations at Port Renfrew during the period of observations. The predicted tide has been subtracted from the record; larger period variations have also been removed by subtracting a combination of spline-fit and polynomial-fit smoothing curve from the data.

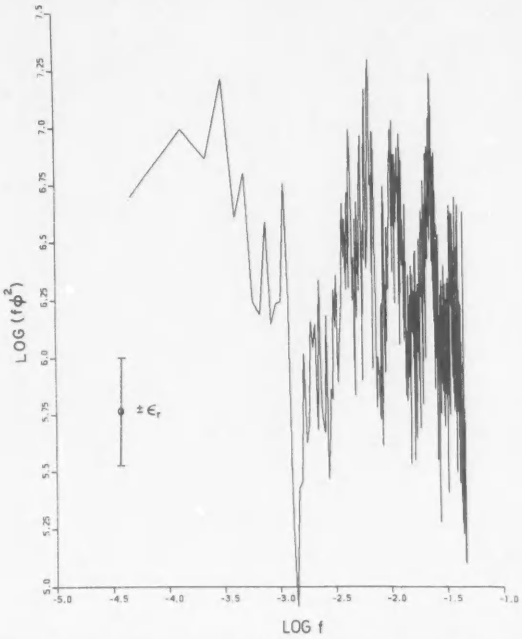

FIG. 3. Power spectrum of the time series of Fig. 2, smoothed over four points. The 95% significance interval $\pm\ \epsilon_r$ is indicated. Frequency f is in Hz, the energy density ϕ^2 in cm^2/Hz.

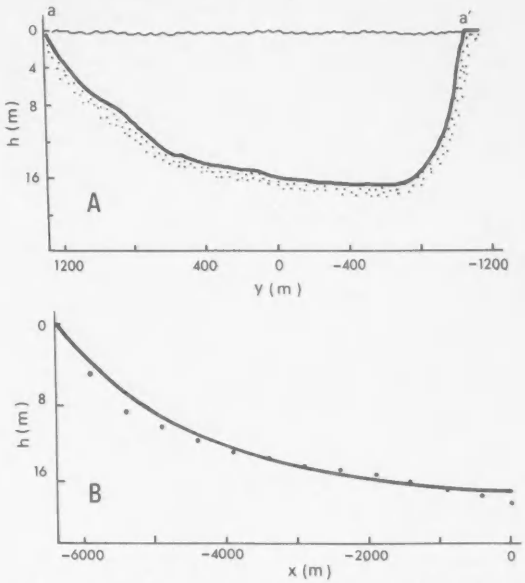

FIG. 4. A) Cross-sectional bathymetric profile of Port San Juan along the line aa′ in Fig. 1; B) Cross-sectionally averaged depth, referred to mean sea level, along the axis of Port San Juan (dots), and its fit by the exponential form given in the text (solid line).

manent tide gauge. The other peaks do not correspond to any periods which stand out in the records. Above the spectral gap (periods from 630 to 10 s) there is a considerable amount of energy distributed in an irregular series of narrow peaks, many of which are significant at the 95% level.

The spectra resulting from the other detrended series (polynomial fit alone, or spline fit alone) show all the low-frequency peaks (below the gap), with the exception of that at 132 min, which is not present in one of them. Since this peak appears at the extreme low-frequency end of the spectrum, where artifacts produced by the detrending process are most likely to show up, it is possible that it may arise as a consequence of the data processing. A power spectrum calculated from the data recorded by the instrument's rapid sampling channel did not show a peak at 132 min, but had all the other low frequency peaks.

Theoretical Model

The origin of the observed oscillations was first sought in the modes of vibration of the waters of Port San Juan. The bay may be idealized as having a rectangular plan form, with a mean width $2w$ ($w = 1000$ m) and length L ($L = 6400$ m). The depth of the bay below mean sea level is obtained by adding 2 m to chart depth (Canadian Hydrographic Service, Tide Tables, Vol. 6, 1974). A typical bathymetric section is shown in Fig. 4a; lateral depth variation will be neglected in the analysis and the laterally-averaged depth h will vary only along the bay. The longitudinal profile of laterally-averaged depth of Port Renfrew is closely approximated by the exponential form

$$(1)\quad h(x) = h_o[1 - e^{-\alpha(x+L)}],$$

where x increases from $x = -L$ at the head of the bay to $x = 0$ at the mouth. The best fit to actual soundings is obtained with $h_o = 16.2$ m and $\alpha = 5 \times 10^{-4} \cdot m^{-1}$ (Fig. 4b). During the period of observations, the water surface was raised 0.6 m above mean sea level at high tide (at 1600 PST) and fell to 0.85 m below mean sea level at low tide (at 0944 PST). The influence of these depth variations will be discussed later.

An analysis of the propagation of long gravity waves along a coast with bathymetry of the form (1) has been presented by Ball (1967). His results are not directly applicable, but his analysis requires so little modification that it will be sufficient for us to state only the problem and its solution, leaving the derivation to be found in Ball's work. For the relatively short periods considered, the influence of the Earth's rotation may be neglected. Including a linear bottom friction term, the linearized shallow-water equations take the form

$$(2a)\quad u_t = -g\eta_x - \lambda u,$$

$$(2b)\quad v_t = -g\eta_y - \lambda v,$$

$$(2c)\quad (hu)_x + hv_y = -\eta_t,$$

where u and v are the velocity components in the x and

TABLE 1. Uncoupled eigenperiods of free undamped oscillations of San Juan Harbour, calculated by setting $\eta(0, y, t) = 0$ in (3). m = transverse mode number, n = longitudinal mode number.

n/m	0 (min)	1 (min)	2 (min/s)	3 (s)	4 (s)
0	36.9	10.2	7.0/417	331	287
1	13.9	6.2	4.1/245	196	167
2	8.7	4.7	3.3/196	156	133
3	6.4	4.1	3.0/178	136	114
4	5.0	3.6	2.8/166	124	103

y directions respectively, η the displacement of the free surface from its equilibrium level, g is the acceleration of gravity, λ is a friction coefficient, and derivatives are indicated by subscripts. We assume a harmonic time dependence of the form $\exp(ivt)$ for all variables. The solutions for η which satisfy $v = 0$ on the side walls, $y = \pm w$, and are bounded everywhere in $x\epsilon[-L,0]$ are written as

$$(3a)\quad \eta(x, y, t) = A\, e^{-\lambda t/2} \cos\nu t \cos\left[\frac{m\pi\,(y - w)}{2w}\right] \times \mathrm{Re}\{e^{-\alpha p(x+L)}\, {}_2F_1[a, b; 1, 1-e^{-\alpha(x+L)}]\},$$

where ${}_2F_1$ is the hypergeometric function (Abramowitz and Stegun 1970, p. 556), A is the amplitude, and

$$(3b)\quad \kappa = m\pi/2\alpha w,\ \sigma^2 = (\nu^2 + \lambda^2/4)/gh_o\alpha^2,\ p = \sqrt{\kappa^2 - \sigma^2},$$
$$a = \tfrac{1}{2}[1 + 2p + \sqrt{1 + 4\kappa^2}],$$
$$b = \tfrac{1}{2}[1 + 2p - \sqrt{1 + 4\kappa^2}].$$

The index m is the transverse mode number and takes the values $0, 1, 2, \ldots$

A simple approximation to the free oscillation frequencies of an open-ended basin in contact with a very large reservoir may be obtained by setting the surface displacement at the mouth equal to zero and neglecting friction (i.e. putting $\lambda = 0$). With appropriate values of h_o, L, α, and w substituted into (3a), equating $\eta(0, y, t)$ to zero gives a relation for the eigenfrequencies $\nu_{n,m}$. Values of the eigenperiods $[T_{n,m} = 2\pi/\nu_{n,m}]$ for the first five transverse (m) and longitudinal (n) modes are shown in Table 1. We note that only two of these periods are longer than that at which the spectral gap occurs in Fig. 3. The influence of tidal depth modulations during the period of observations may be found from the dependence of frequency on $\sqrt{h_o}$, as given in (3b). With the tidal displacements given above, the periods given in Table 1 for mean sea level depths would be increased by 2.7% at low tide and decreased by 1.8% at high tide.

A more accurate calculation of the eigenfrequencies of San Juan Harbour must include friction as well as the coupling between the bay and the ocean. The influence of the ocean on the oscillations of the bay may be characterized in terms of its impedance Z_o (the impedance of the bay will be labelled Z_B), in the equivalent circuit approach introduced by Miles (1971) and also used by Garrett (1975). The maximum response to forcing at the mouth of the bay, by whatever type of oceanic motion, occurs at a minimum of $|Z_o + Z_B|$. The resonant frequencies may be found from this condition.

Low-Frequency Peaks

Distinct peaks are unambiguously identified in the low frequency part of the spectrum. The first approximation (Table 1) to the resonant periods shows that only the first two $m = 0$ modes have frequencies which fall below the spectral gap in Fig. 3. Considering oscillations without y-dependence, the bay may be treated as a small pulsating source giving onto a large ocean. We take the depth of the ocean, H, as uniform and of a value appropriate to the continental shelf region ($\simeq$100 m); a deep-ocean depth value would make the ocean loading completely negligible, so that our choice of H provides an upper bound for the effective oceanic impedance. Using Buchwald's (1971) result, we have Z_o:

$$(4)\quad Z_o = \frac{\nu}{2gH}\{1 - 2i[\ln(\nu w/\sqrt{gH}) + \gamma - 3/2]\},$$

where $\gamma = 0.5772\ldots$ is Euler's constant. The impedance of the bay itself is given by the ratio of surface displacement to mass flux at the mouth:

$$(5)\quad Z_B = \frac{\eta(0)}{2wh_o u(0)}.$$

With an $\exp(ivt)$ time dependence and using (2a), Z_B becomes

$$(6)\quad Z_B = \frac{-(i\nu + \lambda)\eta(0)}{2wh_o g\ \partial\eta/\partial x\,(0)}.$$

Consider first the inviscid case: $\lambda = 0$. The ocean loading introduces a purely resistive term (the real part of Z_1) as well as a reactive term similar to that of the inviscid bay impedance. For the frequencies considered, $\nu w/\sqrt{gH} < 1$, so that the imaginary part of Z_o is positive. When $\lambda = 0$, $|Z_o + Z_B|$ passes through a minimum when the imaginary parts of Z_o and Z_B cancel, i.e. when $\eta(o)/\eta_x(o) > o$, which occurs at a frequency greater than the unloaded resonant frequency for the first mode, smaller for second mode. Thus, although the oceanic impedance might increase the period of the 13.9 min mode of Table 1 towards 14.6 min, it cannot account for a slowing down of the first mode from 36.9 to 38.5 min. Linear friction alone, on the other hand, does not alter the eigenvalues $\sigma_{n,m}$ but decreases $\nu_{n,m}$ through the contribution of λ to σ in (3b). Friction thus works against oceanic loading for the first mode, with it for the second mode. A typical value of the linear bottom friction coefficient is $\lambda = 3 \times 10^{-5}\cdot\mathrm{s}^{-1}$ (Proudman 1953; Jamart and Winter 1978). The undamped frequency of the gravest mode is $\nu = 2\pi/34.1\ \mathrm{min} = 3.07 \times 10^{-3}\cdot\mathrm{s}^{-1}$. Since $\lambda \ll \nu$ the influence of friction on this mode (and a fortiori on the higher modes too) is negligible. The influence of oceanic loading through Z_o has been calculated by Lemon (1975) for a shelf depth of 100 m; the periods of the two gravest modes are modified to 35.5 and 14.5 min,

respectively. Taking into account depth changes due to the tide, the calculated periods range from 34.8 to 36.4 min for the first mode, 14.2 to 14.9 min for the second mode. These periods are close enough to the observed peaks at 38.5 ± 2 and 14.6 ± 0.6 min to conclude that seiche motion at those periods is due to a resonant response of the bay in the first and second longitudinal modes to small excitations at its mouth.

The other two (we do not consider the 132-min peak) significant low frequency peaks, at 21 and 55 min, are not barotropic resonances of San Juan Harbour. A baroclinic response, due to oscillations of the interface between low salinity surface waters resulting from river flow and denser deeper water would have longer periods. However, the pressure variation at the bottom due to a unit displacement at the interface is smaller than that due to a similar displacement at the free surface by a factor $2(\rho_2 - \rho_1)/(\rho_2 + \rho_1)$ where ρ_1 and ρ_2 are the densities of the upper and lower layers respectively. A typical value for that factor in coastal regions is 10^{-2}; thus, for a pressure response equivalent to a peak-to-peak surface variation of 5 cm, a 5 m internal displacement would be required. Such large amplitude internal motions would lead to noticeable surface effects (see LeBlond and Mysak 1978, ch. 36) which were simply not seen from the Port Renfrew Wharf. We thus exclude internal seiches as an explanation of the 55 and 21 min spectral peaks. This leaves only outside perturbations of sea level of amplitudes comparable to those observed in the bay (since resonance is excluded) as a means of explaining these peaks. Cross-channel oscillations of the Strait of Juan de Fuca spring to mind. A straightforward calculation for the gravest mode, using a bathymetric section normal to the entrance of Juan de Fuca and typical of adjacent sections, yields a period of only 15.6 min. Further possible sources of narrow-band sea level displacement signals at the observed seiche periods include bays and headlands along the coast of Vancouver Island (such as Barkeley Sound or the Brooks Peninsula) which could radiate into the ocean, at their own resonant frequency, energy which would in part be trapped as edge waves along the inner part of the continental shelf and travel past the mouth of Port San Juan. A rough calculation, based on quarter-wavelength resonance in a basin of uniform depth, gives a fundamental mode of 54 min for Imperial Eagle Channel, the largest of the openings to the ocean in Barkeley Sound, with mean depth about 50 m and length 18 km. This is close enough to the observed 55-min peak seen in Fig. 3 to lend some credence to the speculation. There are, unfortunately, no high quality sea-level recordings along the outer coast of Vancouver Island from which one could substantiate this speculation by verifying the presence of energy at the observed periods and document the direction of energy propagation along the coast.

Higher Frequency Fluctuation

The energy present in sea-level fluctuation at frequencies above the spectral gap in Fig. 3 is distributed in a series of jagged peaks concentrated in four bands centred on periods of approximately 160, 80, 40, and 20 s. The appearance of energy concentrations at a series of frequency multiples suggests a number of possibilities. The observed periods may represent a series of eigenperiods of a resonant system; they may arise as higher harmonics of a fundamental signal distorted by nonlinear processes, or they may result from some resonant wave–wave interactions. In view of the width of the energy groupings, and in particular because the distribution of eigenperiods of the basin becomes very dense (rather than being distributed in groups of periods) at higher modes, as seen in Table 1, we discard the first interpretation. The first three periods of interest are well above those of the swell observed along that coast; swell of 20-s period is however observed at Tofino (D. Birrell Marine Environmental Data Service, Ottawa, 1976 personal communication), so that the highest frequencies recorded merge with the lower end of the wind wave spectrum. Deformation of incoming swell by shoaling would produce higher harmonics, i.e. oscillations with periods shorter than 20 s, so that we also discard the second mechanism as an explanation of the presence of the observed frequency multiple peaks. Studies of surf beat by Bowen and Guza (1978) and generation of subharmonic edge waves by incoming surf (Guza and Davis 1974) suggest that the energy source for these peaks is a series of wave–wave interactions involving the surf and edge waves, a presumption which can, however, not be verified with the present data.

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Influence of the Shelf-Break Front Off Nova Scotia on Phytoplankton Standing Stock in Winter

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FOURNIER, R. O., M. VAN DET, J. S. WILSON, AND N. B. HARGREAVES. 1979. Influence of the shelf-break front off Nova Scotia on phytoplankton standing stock in winter. J. Fish. Res. Board Can. 36: 1228–1237.

Observations made on the shelf-break front off Nova Scotia during winter on 2 successive yr show the concentration of chlorophyll *a* in the euphotic zone to be correlated to the inclination of the subsurface front. The steepness of the front influences the depth to which phytoplankton are mixed which in turn controls the average amount of illumination received by a given cell. The two winter observations showed the subsurface front at each of two extremes: vertical with little phytoplankton biomass and almost horizontal with significant quantities of chlorophyll. Calculations were made as to the amount of production enchancement that could result from shallowing of the mixed layer by decreased frontal inclination. They show that during the winter under ideal conditions as few as 35 d of intermittent growth increase annual production in the frontal region by 25%.

Key words: front, winter production, phytoplankton, shelf-break, chlorophyll *a*, frontal oscillations, growth enhancement, stability, stratification

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Des observations faites sur le front du rebord du plateau continental au large de la Nouvelle-Ecosse durant 2 hivers consécutifs démontrent qu'il y a corrélation entre la concentration de chlorophylle *a* dans la zone euphotique et la pente du front de profondeur. Le degré d'inclinaison du front influe sur la profondeur à laquelle le phytoplancton se mélange, ce qui, à son tour, règle la quantité moyenne d'illumination que reçoit une cellule donnée. Les observations de ces deux hivers montrent le front de profondeur à l'un et l'autre de deux extrêmes: vertical avec faible biomasse phytoplanctonique et presque horizontal avec quantité appréciable de chlorophylle. Nous avons calculé de combien la production augmenterait si la couche mixte diminuait de profondeur par suite d'une diminution de l'inclinaison frontale. Ces calculs démontrent qu'en hiver, dans des conditions idéales, une période aussi courte que 35 jours de croissance intermittente éléverait la production annuelle dans la région frontale de 25%.

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ALTHOUGH fronts have been recognized as oceanographic phenomena since before the turn of the century (Libbey 1891), oceanographers have until recently devoted little effort towards understanding the biological ramifications of these boundary regions. In addition to compiling a summary of frontal types and characteristics, Uda (1959) described some peripheral biological observations made near Japan. He suggested that fronts sometimes act as floral and faunal boundaries while at other times plankton and particulate material accumulate as a result of convergence. In either case these localized aggregations attract organisms higher in the food chain, a fact which is often exploited by Japanese fishermen. In addition, Uda suggested that fronts have an undetermined stimulatory effect on phytoplankton growth in the spring.

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The most recent work on the biology of fronts has taken place around the British Isles (Pingree et al. 1975, 1976, 1977; Savidge 1976) and has focused on the enhancement of local phytoplankton production by tidally induced mixing. Pingree and colleagues have shown that fronts can act as transitional regions between well mixed-nutrient rich and stratified-nutrient poor areas. The front is characterized by intermittent periods of thermal stability interrupted by periods of nutrient renewal due to wind or tide induced mixing. The final result is a situation conducive to rapid phytoplankton growth.

Fournier et al. (1977) have reported unusually high phytoplankton biomass off Nova Scotia in association with sharp gradients in temperature and salinity. These particular gradients identify the shelf-break front which is the transition from coastal to slope water in that area. Some indirect evidence exists which also suggests enhanced production for this area, notably the abun-

dance of surface-feeding sea birds (Brown et al. 1975) and fishing intensity (Grant and Rygh 1973). Additional evidence obtained further south off the east coast of the United States supports the concept of the shelf break as a distinctly productive region. Observations made on zooplankton (Clarke 1940; Grice and Hart 1962), benthos (Sanders et al. 1965), and fish (Schroeder 1955) show higher levels of standing stocks along the upper slope than are found either shallower or deeper.

Although the data of Fournier et al. (1977) show high phytoplankton biomass in three of four seasons (no peak was observed in late fall) near the shelf-break this report will consider only winter and early spring. During that period the seasonal thermocline has not yet become established and consequently mixing occurs to considerable depths. Nutrients are abundant everywhere and therefore offer no impediment to growth. Light, however, is reduced because of day length, the sun's declination, increased cloud cover, and the average depth to which the phytoplankton are mixed. Availability of light to phytoplankton was shown long ago (Riley 1942) to be the principal factor controlling growth during this period. This paper considers the role of frontal stratification in increasing the amount of light reaching phytoplankton during winter.

Materials and Methods

Observations presented here were made on C.S.S. *Dawson* from March 9–14, 1977 and February 27 to March 3, 1978 along a transect normal to the coast of Nova Scotia (Fig. 1). The first cruise will be considered in detail while the second will be introduced briefly in order to contrast the two winter fronts. Both cruises were identical in terms of regions studied, techniques used, and general approach. They differ somewhat in station location, general weather conditions, and frontal characteristics.

The March 1977 cruise proceeded in two parts: an initial segment from Halifax to just beyond the shelf-break and a second segment on a line continuous with the first but extending seaward a further 185 km. The second segment was traversed twice within 24 h. While the ship was underway, in vivo relative fluorescence and ambient temperature were continuously monitored from water pumped through a hull fitting about 3 m below the surface. Fluorescence and temperature were measured using a Turner Designs model 10 fluorometer equipped with a linear thermistor. Chlorophyll and temperature calibrations were performed at frequent but irregular intervals each day. Conversion of fluorescence to chlorophyll was based on a least-squares linear regression obtained from 34 calibration points where fluorescence $= -0.16 + 4.82$ chlorophyll *a*. Surface temperature measurements were relatively precise but slightly inaccurate due to warming during passage through the ship. Consequently, temperatures presented have been corrected by comparison with independent measurements.

Outbound across the shelf a Guildline (series 8100) analog C.T.D. was used to sample routinely each station (1–10), whereas water bottle samples were taken only at stations 3 and 10. Beyond station 10 a nonstop run was made between 12:21 and 18:05 A.S.T. on March 9. The return to station 10 was made that evening and at 04:40 on March 10 the transect was repeated. This second pass was interrupted by 18 stations at intervals of 5–8 km. Samples at each of these stations were taken using the C.T.D. mounted to a General Oceanics rosette which contained 10, 1.7-L Niskin bottles. The depth of the euphotic zone, i.e. the 1% light level, was determined using either a Lambda Instruments underwater quantum sensor or a Secchi disk.

Water samples from each Niskin bottle were analyzed for salinity (as a check against the C.T.D.), chlorophyll *a*, nitrite, nitrate, ammonia, phosphate and silicate. Chlorophyll *a* was measured fluorometrically using 90% acetone extracts according to Strickland and Parsons (1972). All nutrients were filtered directly through Gelman type A-E glass fibre filters mounted in Millipore® Swinnex filter holders as the water was drained from the Niskin bottles. This filtered water was used to rinse screw-capped tubes. Then 6–8 mL of sample were added and immediately frozen at −40°C. Silicate samples were not filtered and plastic rather than glass tubes were used. All nutrients were analyzed within 1 wk of collection using a Technicon Autoanalyzer II. The tubes into which the samples were placed on shipboard were inserted directly into the instrument sampling tray and thus were handled only once, at the time of collection. Analyses were performed using the recommended Technicon procedure for each nutrient; nitrate and nitrite (Industrial Method 158-71W), nitrite (161-71W), ammonia (154-71W), silicate, and orthophosphate (155-71W).

Because the March 1977 cruise period was remarkably free of cloud cover (1978 was completely overcast) it was possible to obtain good quality infrared satellite photographs (N.O.A.A. V, National Environmental Satellite Service, World Weather Building, Washington, D.C.) for the shelf and slope regions. The photographs were rectified, enhanced and accompanied by a 1:1 digital overlay averaged over 10 km^2. From these data a map was constructed which described the surface temperature field for March 12, 1977. Corrections for atmospheric absorption were not made so the infrared temperatures are slightly less than those observed on shipboard. However, comparison of satellite temperature data with our shipboard ground truth data show no difference greater than 1°C. This is probably due to the exceptionally clear atmospheric conditions experienced on this cruise. In any case, the only use intended for the satellite data is to put the cruise into a overall shelf-slope perspective with regard to the general temperature field.

Results

Winter 1977

Infrared satellite sensors resolved the waters around Nova Scotia on March 12, 1977 into thermally distinct areas (Fig. 1). Each area, except for 7, has a uniform but narrow temperature range. Area 7 shows itself, through the range of temperatures observed, to be a region of intense mixing. This is in keeping with the definition of slope water by McLellan et al. (1953) as a region characterized by mixing of coastal water and Gulf Stream. Perhaps the most outstanding feature of Fig. 1 is the apparently discontinuous nature of slope water. Because this water appears as a long southerly intrusion, the cruise transect (stations 1–33) passed from coastal water through slope water and

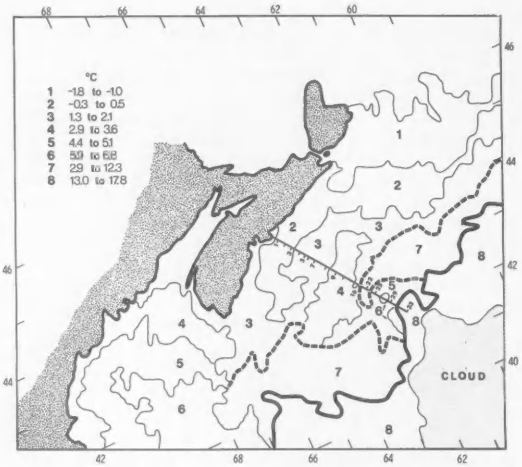

FIG. 1. Surface temperature field off Nova Scotia on March 12, 1977. Large numbers (1–8) correspond to temperature ranges indicated in legend. Straight line normal to coast shows cruise transect and selected station locations (1–33). Dashed line is shelf-break front at northern edge of slope water (7) and heavy solid line is boundary to water (8) strongly influenced by Gulf Stream. Further offshore, atmospheric cloud cover obscured sea surface thermal observation.

back into coastal water prior to entering the uniformly warmer water to the east.

Figure 2 presents temperature, salinity, and sigma-*t* isopleths for the entire cruise transect. The three presentations are quite similar and both independently and collectively show the shelf-break front to be located between stations 16–21. The distance separating those stations is only 25 km, but surface temperatures, salinity, and densities increased from 3 to 8.5°C, 32.0 to 34.6‰, and 25.5 to 26.5 sigma-*t* units, respectively. The subsurface front is visible as a distinct vertical gradient which slopes back toward the coast, gradually becoming deeper, and eventually intersecting the sea floor about 40 km from Halifax. Because of this deepening frontal boundary only stations 1 and 2 are purely coastal water (Fig. 3) while all remaining stations (out to and including station 30) are composed of coastal and slope. The upper 35 m across the shelf show little stratification except for station 3 where the density structure suggests a small front.

Between stations 16–21, i.e. directly in the middle of the shelf-break front, very sharp vertical gradients were visible in all three variables (Fig. 2 and 3). The gradients were sharpest over the upper 20 m but extended to almost 50 m. By contrast, station 22 is practically isothermal and isohaline to 50 m (Fig. 2 and 3). In the upper 20–30 m of stations 23–29 temperatures (T) and salinities (S) were higher than those on the shelf but nevertheless a clear affinity exists with shelf water based on similarity of T/S characteristics (Fig. 3). The upward bending isotherms and isohalines at stations 25–28 demonstrated two small fronts at approximately 290 and 310 km offshore. Finally, between stations 30 and 31 the final and most dramatic front was encountered. Temperature and salinity increased approximately 10°C and 3.5‰. Beyond station 31 the water was isothermal and isohaline to greater than 100 m, indicating that we had entered water with a very strong Gulf Stream component. All of the above transitions are consistent with the general temperature field shown in Fig. 1.

Surface temperature and chlorophyll *a* obtained continuously along the transect are presented in Fig. 4 as a single shelf trace and two replicate slope traces. On the shelf portion chlorophyll *a* was reasonably constant, varying around an average value of 1.27 ± 0.06 mg·m^{-3}. The only important deviation occurred between 40–60 km offshore where chlorophyll *a* increased to 2.5 mg·m^{-3} coincident with the small front shown in Fig. 2. Surface temperature increased gradually and steadily (except at the previously mentioned front) across the shelf from −0.5°C to almost 4° just beyond the shelf break.

The general trends in chlorophyll *a* visible along the two slope transects are as follows: a sharp increase (to 4.5 mg·m^{-3}) coincident with a 6.5°C temperature rise, a sudden drop (to 1.0 mg·m^{-3}) upon entering the well mixed slope water (Stn. 22) followed by additional peaks (to 2.5 mg·m^{-3}) in mid-transect where a slight temperature increase was recorded due to the upward bending isotherms (Stas. 25–28) and finally the lowest values observed on the entire cruise (0.5 mg·m^{-3}) were encountered coincident with our passage into the warmer water to the east. The mean and 95% confidence interval for the slope transect was 1.79 ± 0.22.

The remaining frame in Fig. 4 presents chlorophyll *a* m^{-3} obtained using bottles from 5 m at every station plus a value for chlorophyll *a* m^{-2} integrated from 5 to 20 m. The similarity of these two curves with the continuous chlorophyll record substantiates the view that on this cruise the continuously monitored values reflect the euphotic zone as a whole and not just a thin upper layer.

Over the length of the entire transect all five of the nutrients monitored (Table 1) were high and reasonably consistent despite the remarkable hydrographic variability. Nitrates, for example, varied between 4–9 μmol/L which is usual for surface waters in winter (Fournier et al. 1977). These concentrations were all above the level where nitrate exerts any limitation on growth rate (Eppley et al. 1969). Even though increased chlorophyll *a* was observed at several locations the high nutrient levels suggest that either accelerated growth had not been underway for very long or that some intermittent resupply was occurring through vertical or lateral mixing. Otherwise within several days of the onset of rapid growth the nutrients would show some sign of utilization.

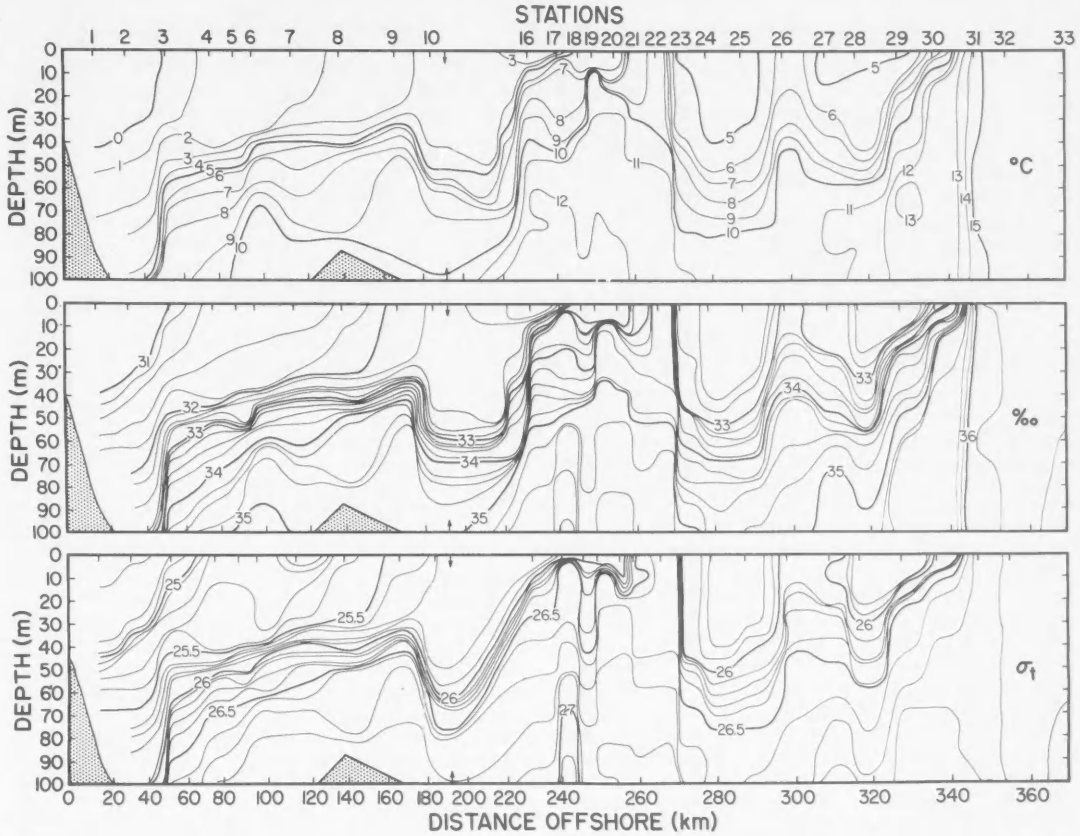

FIG. 2. Temperature (°C), salinity (‰), and density (σ_t) profiles over 1977 cruise transect. Small arrow between 180–800 km offshore indicates location of shelf break; horizontal scale expands beyond 220 km.

VERTICAL STABILITY

Some indication of the extent of vertical mixing can be obtained by examining density gradients at each station, because the change in vertical direction of sigma-*t* is nearly proportional to vertical stability (Sverdrup et al. 1942). Table 2 presents two simple and complimentary expressions of vertical stability. First, the difference in sigma-*t* between the surface and 25 m (i.e. the average depth of the euphotic zone) was calculated. The range in values extends from −0.08 (Stn. 23) to 0.97 (Stn. 16) and reflect conditions observed both in slope water and the front, respectively. These numerical estimates of stability merely reinforce what is visually obvious (Fig. 2), i.e. that the inclined nature of the front presents a strong barrier to vertical mixing. This barrier is not present in the slope water and the negative sigma-*t* values observed there indicate a condition of instability, i.e. mixing was underway at the time of observation.

The second approach used in Table 2 was to determine the depth of water that was required to observe a change of 0.2 sigma-*t* units. The value of 0.2 was selected because it was the smallest change that could be accurately measured at the four most heavily strati-

TABLE 1. Mean nutrient concentrations (μmol/L) from the euphotic zone (0–20 m) at selected stations over shelf and slope

Stn.	NO_3	NO_2	NH_3	PO_4	SiO_2
3	6.4	0.3	1.1	0.9	6.3
10	5.6	0.5	0.6	0.7	3.9
16	5.4	0.7	1.9	1.0	3.8
18	6.4	0.7	1.4	0.9	3.4
20	6.3	0.3	0.6	0.8	2.3
22	8.4	0.3	0.9	0.9	4.7
24	4.4	0.3	0.7	0.7	3.2
26	5.2	0.3	0.6	0.7	3.8
28	4.1	0.4	0.9	0.8	3.0
30	6.1	0.2	2.0	0.6	3.3
32	6.5	0.6	0.7	0.6	3.1

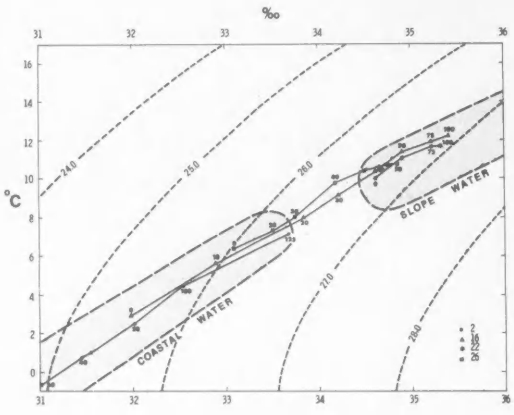

FIG. 3. Temperature–salinity diagram from four selected stations. The two envelopes broadly define coastal and slope water, while the space between the envelopes is the subsurface frontal zone.

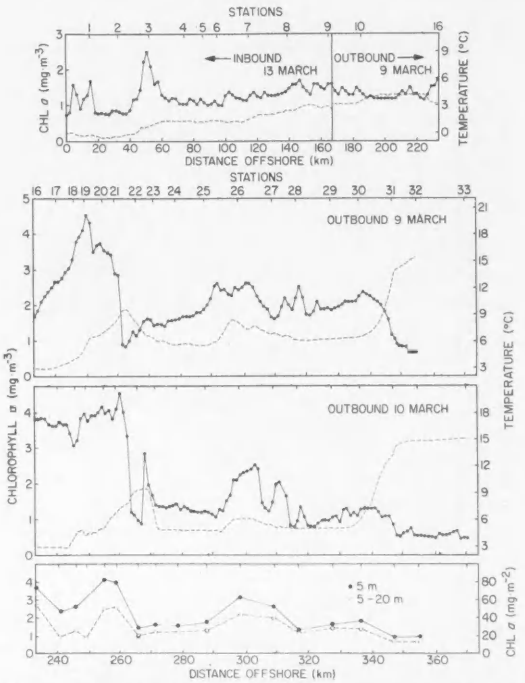

FIG. 4. The upper three frames show continuous records of temperature (dashed line) and chlorophyll *a* plotted against distance offshore. The upper frame extends from the coast to just before the front and is a composite of inbound and outbound traces. The next two frames are replicates which extend the transect out through the front to 350 km offshore. The final frame shows chlorophyll *a* extracted from sea water samples collected at stations on replicate transects and presented as a single value from 5 m and an integrated value from 5 to 20 m.

fied stations (4, 16, 17, and 19) and also it represented a crude approximation of the surface mixed layer. Both approaches yield essentially the same result (Table 2), i.e. high chlorophyll appears in most cases to be coincident with high stability (e.g. Stn. 3, 16–20, and 26). Conversely, where stability is low and mixing more intense then chlorophyll is proportionately lower (e.g. Stn. 22 and 31–33). There are exceptions to this generality (e.g. Stn. 21, 29, and 30) and they will be considered below.

Figure 5 represents a least-squares linear regression which shows the relationship between chlorophyll *a* concentration and the sigma-*t* gradient between 0–25 m. (A similar correlation was attempted between chlorophyll *a* versus the first derivative of temperature for the entire transect but this yielded a slope of 0.01 and r^2 of 0.00). According to this analysis (significant at 95% confidence interval) 40% of the observed variability in chlorophyll *a* can be accounted for by change in sigma-*t* alone. Three points account for much of the unexplained variability. If the data from stations 21, 29, and 30 (which gave residuals of 3.08, 2.30, and 1.91 standard deviations from the mean) are omitted from the regression then r^2 increases to 0.88.

Although the above points were not excluded some evidence exists to suggest that they might be considered separately. The three data points either have very high chlorophyll with low stability (Stn. 21) or very low chlorophyll with high stability (Stn. 29 and 30). All three have in common the fact that they are immediately adjacent to well mixed regions with negative sigma-*t* gradients. We feel that these three stations depart from the trend observed in the remainder of the data because of a lag time between phytoplankton abundance and water movement. Stations 29 and 30 may have recently stabilized but still had not had sufficient time to produce chlorophyll levels similar to those observed between stations 16–20. Station 21 could have achieved growth followed by a sudden loss of stability and our measurements made before the evidence of the growth had dissipated.

WINTER 1978

Figure 6 summarizes the chlorophyll *a* and hydrographic data obtained on the same transect almost exactly one year later. On this cruise in 1978 nutrient and seasonal light levels were similar to 1977 except that the latter cruise was heavily overcast with high winds (50-110 km·h^{-1}) throughout. Similarities between the cruises include almost identical onshore–offshore gradients in temperature and salinity, a small front about 60 km off the coast plus a shelf-break front (4–13°C and 33.2–35.5‰) slightly further offshore (300 vs. 240 km).

Differences between cruises include chlorophyll *a*

TABLE 2. Two complimentary calculations expressing vertical density gradients and surface chlorophyll *a* (milligrams per cubic metre) at all stations on 1977 cruise. The first density calculation is the depth in metres over which a difference of 0.2 sigma-*t* units occurred while the second ($\Delta\sigma_t$) is the difference in density between the surface and 25 m in sigma-*t* units.

Stn.	Depth	$\Delta\sigma_t$	Chl	Stn.	Depth	$\Delta\sigma_t$	Chl
1	40	0.09	1.7	20	10	0.73	4.0
2	32	0.08	0.9	21	57	0.08	4.1
3	11	0.31	2.3	22	59	−0.06	0.8
4	42	0.09	1.1	23	49	−0.08	1.4
5	44	−0.04	1.1	24	55	−0.01	1.4
6	37	0.02	1.1	25	37	0.00	1.2
7	17	0.27	1.2	26	19	0.28	2.3
8	31	0.08	1.4	27	19	0.23	1.8
9	28	0.09	1.6	28	27	0.16	1.2
10	60	0.02	1.5	29	12	0.88	1.1
16	7	0.97	3.8	30	4	0.75	1.3
17	5	0.81	3.7	31	>100	−0.03	0.7
18	10	0.48	3.2	32	>100	0.00	0.6
19	6	0.81	3.9	33	>100	0.00	0.5

concentrations across shelf and slope which averaged 0.67 ± 0.03 mg·m^{-3} and nowhere exceeded 1.2 mg·m^{-2} while in 1977 the respective values were 1.55 $\pm$ 0.12 to a maximum of 4.5 mg·m^{-3}. Three outstanding peaks were visible: between Stn. 3–4 (1.17 mg·m^{-3}), Stn. 12–19 (0.87 mg·m^{-3}) and Stn. 17 (0.72 mg·m^{-3}) while once again the lowest values on the transect (0.16 mg·m^{-3}) occurred in the warmer water east of the front. Each of these chlorophyll peaks is associated with gradients in sigma-*t* visible in Fig. 6. Perhaps the most important difference between the shelf-break fronts in both years is the inclination of the subsurface component as it leaves the air–sea interface and proceeds inshore. In 1977 it sloped sharply almost becoming horizontal in some places while in 1978 it was vertical. This difference in slope greatly influences the mixed layer depth. In 1977 over the 25 km inshore of the 9°C surface isotherm (Stn. 16–20), the necessary depth to obtain a difference of 0.2 sigma-*t* units was 8 m. In 1978 over a slightly greater distance but the same temperature range (40 km, Stn. 16–18) it was 42 m. Hence in 1977 the phytoplankton inshore of the 9°C isotherm were mixing over 0.3× the depth of the euphotic zone while in 1978 it was 1.7×, a more than fivefold increase.

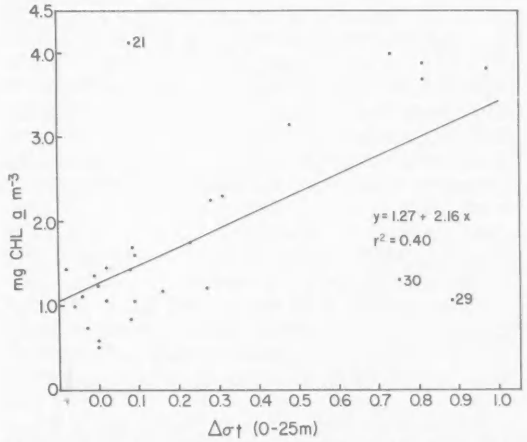

FIG. 5. Least-squares linear regression of chlorophyll *a* on the difference in density ($\Delta\sigma_t$) from 0 to 25 m at all stations on 1977 cruise.

Discussion

The traditional explanation of seasonal phytoplankton dynamics in temperate regions is that following the autumnal flowering, vertical mixing due to storms or nighttime cooling is intensified to the point where plants become light limited. During this period nutrients are mixed upward and levels of nitrate and phosphate reach their annual euphotic zone maxima (Riley 1946). Late fall and winter are usually thought of as periods of limited growth punctuated by short, sporadic outbursts which result from intervals of thermally induced stability. With the approach of spring and increasing insolation these outbursts become more frequent. When permanent stratification finally arrives in the spring, growth proceeds rapidly until nutrients are exhausted and, except for occasional mixing events which can inject nutrients into the euphotic zone, phytoplankton standing stocks remain at a modest level throughout the summer.

Therefore, during late fall and winter phytoplankton growth is not limited by nutrient availability but rather by a shortage of light resulting in part from increased mixing to greater depths. It follows then that any physical process which acts either to reduce the depth of the mixed layer or retain phytoplankton closer to the surface will in effect increase the amount of light available for photosynthesis. This is, of course, embodied

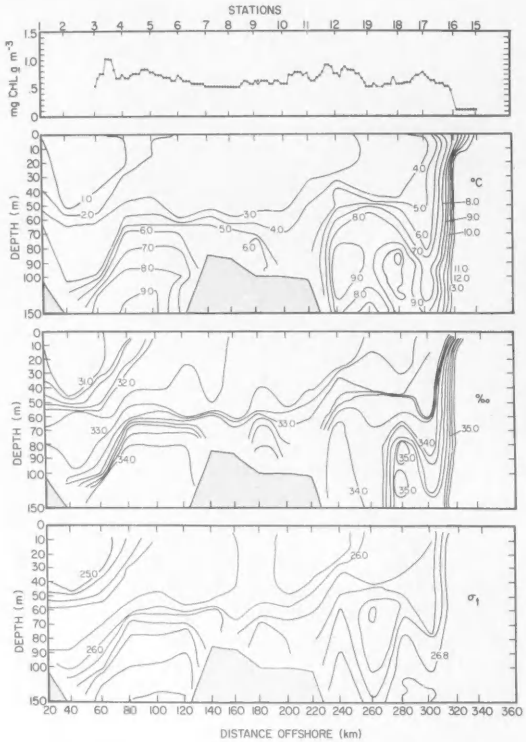

FIG. 6. Chlorophyll *a*, temperature (°C), salinity (‰), and density (σ_t) profiles over 1978 transect. Horizontal scale uniform across transect, in contrast to Fig. 2. This transect was discontinuous. Following Stn. 12 the ship proceeded offshore and stations were run as on the return.

in the critical depth concept described by Riley (1942) and later by Sverdrup (1953). From the 1977 data it appears that the shoreward sloping subsurface front provides just such a barrier to vertical mixing. The most intense phytoplankton activity was noted just inshore of slope water where the mixed depth was shallowest. With increasing distance away from the 9°C isotherm, the frontal zone steepened, the depth of the mixed layer increased, and phytoplankton biomass gradually leveled off.

Although the shelf-break front is the most dramatic display of mixed layer reduction, other lesser examples are also available. Near station 3 chlorophyll *a* concentrations were higher because mixing was reduced by 60% compared to stations on either side. Also, offshore in the vicinity of stations 26–28 (Fig. 2 and 4) a similar result was achieved when slope water intruded upward. The only front on the transect where the mixed layer was reduced but chlorophyll was low occurred between stations 29–30. The presumed reasons for their nonconformity have already been mentioned.

From late fall to early spring, water on the shelf is colder than that over the slope with the result that the shelf-break front is well defined and clearly visible with both satellite infrared imagery and shipboard temperature observations (Fournier et al. 1977). Both cruises under discussion support this observation. However, although the front is a prominent, clearly defined boundary at least 5 mo of the year the location and inclination of the subsurface component appears to be quite variable. The chlorophyll data from both cruises clearly reflects that variability. Despite these year-to-year differences some evidence was presented earlier which supports the concept of the upper slope as a region of selectively enhanced production. Measurements and observations were made at several levels in the food chain, from primary production (Fournier et al. 1977) to fish and surface-feeding sea birds (Schroeder 1955; Brown et al. 1975). In addition, B. T. Hargrave (Bedford Institute, personal communication) has observed sediment chlorophyll values on the upper slope, beneath the average position of the front, to be 30× greater than that measured at either greater or lesser depths. Mills and Fournier (1979), using limited data, estimated this production enhancement at between 10–25%. Considering the two extremes in subsurface frontal inclination the question must now be asked whether the high chlorophyll observed in 1977 is an intermittent ephemeral contribution or part of a predictable continuum which contributes to the observed enhancement in production.

Changes in mixed layer depth near the front have been shown to be related to the inclination of the subsurface front. The degree of inclination reflects the degree of slope water intrusion toward the coast. Although these intrusions have been well documented (Liem and Hachey 1935; Hachey 1953; McLellan 1957; Houghton et al. 1978) little is known about either their frequency or the symmetry of any one intrusion. Estimates of the frequency of occurrence range from 15 (Houghton et al. 1978) and 60 d (Smith 1978) depending on the forcing mechanism. Despite these limitations in our knowledge of frontal movement we shall attempt to calculate the enhanced production that could be expected in an oscillating system as compared to one which does not oscillate, and by interpolating between these conditions an estimate of frequency might be inferred from the biological data.

Production was calculated using the model which Horwood (1975) found useful in Scottish lakes. The model that follows is identical to Horwood's except that the symbols have been changed for our convenience. The average daily increase in chloorphyll *a* (Chl_{t+1}), over a variable mixing depth (D) is calculated each day using the expression:

$$Chl_{t+1} = Chl_t \cdot 2^{(\mu-\rho)}$$

where ρ is algal respiration set at 10% algal growth (Steele 1965) and μ is the instantaneous rate of doubling calculated for the entire population in the mixed

TABLE 3. Summary of variables measured and calculated, which were used to compute changes in chlorophyll in the frontal region.

	Inclined	Vertical
Mixed layer (D)	8 m	42 m
Extinction coeff. (k)	0.17 m^{-1}	0.17 m^{-1}
Incident light (I_o)	0.15 ly·min^{-1}	0.15 ly·min^{-1}
Light at max. photosynthesis (I_m)	0.05 ly·min^{-1}	0.05 ly·min^{-1}
Maximum doublings (μ_m)	0.63 d^{-1}	0.63 d^{-1}
Nutrient coeff. (Q)	0.88	0.88
Chlorophyll·m^{-2} (Chl_t)	5.0 mg	26.5 mg

layer. It is given by the following equation:

$$\mu = \frac{Q \cdot \mu_m \cdot e^1}{D \cdot K} [e^{-I_o/_m \cdot e^{-KD}} - e^{-I_o/I_m}],$$

where Q is a modifying factor which depends on the level of available nutrients and takes the form of the Monod Equation $Q = S/K + S$. S is the nutrient level given in μmol $NO_3 \cdot L^{-1}$ and K is the half-saturation coefficient. Parameter μ_m is the temperature-dependent maximum rate of doubling calculated as $\log_{10}\mu_m = 0.0275T - 0.07$ (Eppley 1972) where T is temperature in degrees Celsius. Since μ_m was derived from 24 h laboratory experiments it is divided by two to approximate a 12-h day. Parameter k is the extinction coefficient calculated from $k = 1.7/d$ where d is the depth of disappearance of the Secchi disk, I_o is surface radiation, I_m is the radiation level at which maximum photosynthesis occurs.

The calculations which follow were made assuming an average mixed layer depth of 8 m in 1977 and 42 m in 1978. This was the average depth over which a change of 0.2 sigma-t units was observed. The period over which these calculations were made was 120 d, i.e. between December 15 and April 15. Examination of past records (Fournier et al. 1977 and unpublished data) show this interval to be generally unstratified. During this period phytoplankton are mixed deeply and hence are most probably light limited.

Table 3 presents the variables that were used to make production estimates. Mixed layer depth is described above. Extinction coefficients are identical for both conditions and represent a median between the extremes that could be expected when chlorophyll varies from 0.5 to 4.5 mg·m^{-3}. Extinction coefficients can be adjusted for absorption by phytoplankton (Riley 1975) but this was felt to be an unnecessary refinement. The assumed value for incident light is a median value for this latitude (Riley 1946) during the 120 d interval. The light level at the depth of maximum photosynthesis was estimated from simulated in situ production experiments and light measurements made in February 1976 and represent an average of the 50 and 20% light levels. Maximum growth rates were calculated over the 3°C (0.51 doublings) to 9°C (0.75 doublings) temperature range and averaged to 0.63 doublings per day. To calculate the nutrient coefficient Q we used a mixed layer nitrate concentration for February of 7 μmol/L and a half-saturation constant of 1.0 μmol/L suggested by Eppley et al. (1969) for mixed populations in euthrophic conditions. Chlorophyll per square metre of mixing depth was calculated by utilizing the average chlorophyll concentration per cubic metre from the 42 m mixed layer at stations 17 and 18 in 1978. This number (0.6 mg Chl $a \cdot m^{-3}$) was then multiplied by the depth of the mixed layer.

Using the values presented in Table 3 an estimate of Chl_{t+1} was made for the 42-m water column yielded 30.02 mg Chl $a \cdot m^{-2}$ or an increase ($Chl_{t+1} - Chl_t$) of 3.52 mg Chl $\cdot m^{-2} \cdot d^{-1}$. This deeply mixed winter condition probably represents a steady state where daily increases are roughly balanced by losses due to grazing and sinking (Riley 1946). If this were not so then the population would either gradually increase or diminish to a level of undetectability. Daily losses normalized per cubic metre are then 0.08 mg Chl a settled or grazed $\cdot d^{-1}$ and will be used in the following section.

Daily increments in Chl_{t+1} were then calculated for an 8 m mixing depth (observed in March 1977), yielding 0.97 mg Chl $\cdot m^{-2} \cdot d^{-1}$ [$Chl_{t+1} - Chl_t - (\text{loss} \cdot m^{-3} \times 8$ m)]. This increment is the population increase in 24 h. (This represents 0.15 mg Chl $a \cdot m^{-3} \cdot d^{-1}$ or about double the rate for the 42 m column). If conditions do not change then the phytoplankton will continue to grow exponentially until nutrients are depleted or grazing pressure increases in response to the newly available food. However, in winter on the Scotian Shelf the average storm frequency is 2.5–7 d (Petrie and Smith 1977). For our purpose we shall assume an average of 5 d. Csanady (1976) suggests that strong winds operating on an inclined front will reduce stratification and deepen the mixed layer. During this period of increased mixing phytoplankton would be carried deeper thereby reducing available light. Also, increased mixing laterally as well as vertically would reduce the average quantity of chlorophyll per cubic metre, approaching those steady state values observed outside of the frontal region. In effect, these winter storms would act as periodic interruptions in exponential growth. We assume therefore that phytoplankton would grow an average of 5 d in the near-surface stratified layer before that layer was disturbed. Therefore, we extend the cumulative growth rate at 8 m for a period of 5 d. We further assume that zooplankton grazing would not significantly increase over these intermittent 5-d bursts.

Our final calculation is an estimate of the number of 5-d intervals of cumulative growth that would be required in order to augument production levels by 10–25% (Table 4). This calculation for 25% augumentation is simply

$$\frac{(Chl_{t+5} - Chl_t)\,(X \text{ intervals})}{(Chl_{t+1} - Chl_t)\,(120 \text{ d})} \times 100 = 25\%$$

with a numerator representing a stratified, productive 8-m mixed layer and the denominator a steady state 42-

TABLE 4. The number of 5-d intervals between 8 and 42 m required to achieve growth 10 and 25% greater than steady-state losses. Chl_t is the quantity of chlorophyll *a* (milligrams per square metre) present over the various mixed layer depths, μ is the average doubling time (per day) throughout the mixed layer, Chl_{t+5} is the amount of chlorophyll *a* (milligrams per square metre) produced in 5 d above steady-state losses.

Mixed layer				Intervals	
Depth	Chl_t	μ	Chl_{t+5}	10%	25%
8	5.0	0.46	9.4	4.5	11.3
10	6.3	0.46	13.1	3.2	8.1
15	9.5	0.43	16.1	2.6	6.6
20	12.6	0.37	14.0	3.0	7.5
25	15.6	0.32	10.5	4.0	10.1
30	18.9	0.27	7.3	5.8	14.5
35	22.1	0.23	5.1	8.4	20.9
40	25.2	0.21	2.2	19.5	48.7
42	26.5	0.20	0	—	—

m mixed layer. This yields an estimate of 11.3 intervals (or approximately 57 d) for 25% and 4.5 intervals (22 d) for 10%. These values represent the conditions observed in 1977 and 1978. If we now interpolate between 8 and 42 m we can gain some appreciation for the impact of the front on the depth of the mixed layer.

Table 4 shows that although growth rate (μ) decreases with increasing layer depth the increase in chlorophyll per square metre more than offsets this. The result is that a shallowing of the mixed layer to no more than 25 m can produce a chlorophyll increase equivalent to that observed at 8 m. A reduction of the mixed layer to 17.5 m yields the maximum rate of augmentation of new plant material. Therefore, the number of 5-d intervals necessary to achieve a 25% increase in growth declines from 21 at 35 m to 6.6 at 15 m. Any reduction in the depth of the mixed layer will increase growth but a reduction to between 15–20 m can produce a remarkably rapid response.

These calculations serve to explain the enhanced production on the upper continental slope in winter in terms of increased stratification resulting from subsurface frontal movement. The calculations performed above encompass actual observations at two extreme frontal positions, i.e. when the front is vertical (42 m) and when it is almost horizontal (8 m). Verification of the above conceptual model depends on advances in dynamical physical oceanography concerning both the frequency and symmetry of oscillations of the subsurface front.

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Growth and Mortality of the Blue Mussel (*Mytilus edulis*) in Relation to Environmental Indexing[1]

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FREEMAN, K. R., AND L. M. DICKIE. 1979. Growth and mortality of the blue mussel (*Mytilus edulis*) in relation to environmental indexing. J. Fish Res. Board Can. 36: 1238–1249.

Comparative production estimates of selected species may provide indices of environmental quality, but so far there is little information on the extent to which production responses are mediated by genotypes. This study used a single source stock of blue mussels (*Mytilus edulis*) to explore differences between two bays. Test animals were held in suspension for 20 mo and growth and mortality observations of size-groups and of identified individuals were made at biweekly intervals. Average growth rates differed slightly between bays but mortality differences were marked and were the principle determinants of net production differences between the bays. Observed growth rates differed markedly between individuals but showed a striking consistency within individuals, indicative of genetic influence on this parameter. Because both mortality and growth interact with body size and season, it is clear that the estimated production levels and differences between bays would be influenced by the mixture of genotypes. We conclude that growth and mortality measures of *M. edulis* could provide sensitive environmental indices, but growth types in the test stock would need to be standardized.

Key words: mussel; growth, mortality; environmental indices; genetic influence

FREEMAN, K. R., AND L. M. DICKIE. 1979. Growth and mortality of the blue mussel (*Mytilis edulis*) in relation to environmental indexing. J. Fish. Res. Board Can. 36: 1238–1249.

Des estimations de production comparatives d'espèces choisies peuvent fournir des indices de qualité de l'environnement, mais jusqu'à maintenant, on a très peu d'information sur le rôle des génotypes dans les réponses. Nous avons utilisé un stock unique de moules bleues (*Mytilus edulis*) pour étudier les différences entre deux baies. On a maintenu des moules en suspension durant 20 mois et observé, à intervalles de 2 semaines, la croissance et la mortalité de groupes de taille et de sujets marqués. Le rythme de croissance moyen diffère légèrement entre les baies, mais il y a différences marquées dans le mortalité, facteur en grande partie responsable des différences dans la production nette des deux baies. Les rythmes de croissance observés diffèrent notablement entre individus mais, chez un même individu, exhibent une uniformité frappante, signe d'une influence génétique sur ce paramètre. Comme il y a interaction tant de la mortalité que de la croissance avec la grosseur du corps et la saison, il est clair que les niveaux de production estimés et les différences entre les baies sont influencés par le mélange de génotypes. Nous concluons que des mesures de croissance et de mortalité de *M. edulis* seraient des indices sensibles de l'environnement, mais que les types de croissance du stock expérimental devront être normalisés.

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THERE is a need for indices of biological productivity of coastal waters to use in assessing the impact of human activity on environmental parameters. Such indices might allow prediction of the potential for aquaculture, make it possible to monitor progressive changes in environmental quality, or assist in judging the relative merits of alternative forms of public or private use.

The basic information needed is production measurements of one or more reference organisms. Once a satisfactory description of biological production in an area has been developed, it may be possible to index it by using simpler correlated physical, chemical, or biological phenomena. We are concerned here with the problems of defining useful production characteristics of common organisms from the macrofauna.

The blue mussel, *Mytilus edulis*, is a conspicuous worldwide member of the littoral zone (Hutchins 1947) and is considered a potential "sentinel" organism of marine coastal environmental assessment (Goldberg et al. 1978). As with other wide-ranging species, growth rates and population densities vary considerably from place to place. It is this combination of sensitivity to, but tolerance of, a wide variety of environmental conditions that marks it as a species with potential for both

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aquaculture and environmental monitoring. However, because of the possibly long separation of stocks from various bays (Levinton and Koehn 1976) it is necessary to identify and measure the extent to which phenotypic responses to environmental parameters are mediated by genotypic differences.

This paper explores the differences in growth and mortality patterns of mussels taken from a single source stock and reared under different environmental conditions. Observations of productivity over a 20-mo period showed differences between seasons and areas. Each individual mussel used in the experiment was identified and observation of the growth rates of individuals revealed persistent patterns indicative of genotype differences within the source stock. Furthermore, there were important differences in mortality from place to place. The results suggest that it should be possible to utilize the growth and mortality patterns together to enhance the sensitivity of environmental comparisons, but that any index is liable to significant effects of differing genetic constitutions even within a single source stock.

Materials and Methods

Source of Material

In February 1971 mussels were collected from the Northwest Arm of Halifax Harbour, not far from the Bedford Institute of Oceanography, and separated into four shell length-groups as follows: ½–¾ inch (13.7–19.1 mm); 1–1¼ inches (25.4–31.8 mm); 1½–1¾ inches (38.1–44.5 mm); and 2–2½ inches (50.8–63.5 mm). Each size-group contained 25 individuals and each animal was identified by a number cut into the left valve. Cages of ¼-inch (6.4-mm) plastic mesh containing each of these length-groups were suspended in Bedford Basin in front of the Institute (44°40.80′N, 63°36.53′W) at each of three depths: the surface, 2 m, and 5 m. One set of the length groups was suspended at the surface on the eastern edge of neighboring St. Margaret's Bay (44°35.22′N, 63°55.97′W).

Field Procedure

The Bedford Basin growth experiment was started in early March and the St. Margaret's Bay experiment in mid-April of 1971. At 2–3-wk intervals, depending on weather conditions, the cages were retrieved, the shell length of each surviving individual was measured to the nearest 0.1 mm, and a record made of mortalities. All cages were cleaned of epiphytic algal growths and the surviving mussels resuspended. Final measurements were made of all surviving animals in late October of 1972.

Control Experiment

Throughout the experiment animals were subjected to some treatments which were not in keeping with their natural experience and which, though of minor importance perhaps, might have affected growth or mortality. As the main experiment progressed and mortalities began to appear a subexperiment was initiated, designed to test the effects, if any, of the various treatments and handling procedures on production parameters.

Of principal concern here was the frequent severing of the byssal fibres which was necessary to allow shell measurements to be taken. This undoubtedly resulted in each animal spending extra energy to reattach — energy which might otherwise have gone into growth activity. The damage resulting from cutting numbers into the shells was also examined, since substantial accumulations of nacre were noted on the inside of the left valve of dead experimental animals. Furthermore, though the animals tend to gather in clumps in cages (as they do in nature), it was decided to test the effect on production parameters of separation of individuals versus allowing them to clump. Eight combinations of these treatments were established as is indicated in Table 1.

This subexperiment was initiated May 15, 1972, when 25 mussels of the 1–1¼-inch (25.4–31.8-mm) length-class were placed in each of the eight test lots. Growth and mortality were monitored for 7 mo thereafter. "Separated" mussels were held in individual sections of plastic egg containers. "Grouped" animals were placed in cages similar to those used in the main experiment. The animals were held at the surface in Bedford Basin adjacent to the main experiment. "Disturbed" mussels were removed from their attached positions at 2-wk intervals during the experiment and their cages were cleaned. All remaining cages were cleaned as well as possible without dislodging the animals from their byssal attachments.

The Information Statistic (see Methods) was used in place of the χ^2 distribution for analyzing the mortality data. The three alternative classifications of the data in Table 1A were arranged in a series of three 2×2 contingency tables. Thus, the mortalities in the separated and grouped categories were found to be homogeneously distributed between disturbed and undisturbed or between numbered and unnumbered animals. However, mortalities in the disturbed and undisturbed categories were not homogeneously distributed between the numbered and unnumbered categories due to the relatively high mortality in the disturbed-unnumbered category of both separated and grouped animals. We cannot explain the intensity of mortality in this treatment, but note that 40% of it took place in the first month of the experiment, compared with about 10% in the first month in other treatments. We infer that the mortality in this lot was unrelated to the experimental procedures, hence that the "subexperiment" indicated no mortality effects of the procedures. Similarly, the growth data (Table 1B) showed no appreciable effects of the treatment procedures on growth rates.

Accumulations of nacre on dead shells proved to be due to infestations of the mud-worm *Polydora websteri*. Infestation was highest in the "numbered" groups confirming that the intensity is related to periostracum injury. Not only was the incidence higher in the numbered animals (84.8%) versus unnumbered (41.9%), but the infestation was much higher in the left (numbered) valves (92.9 vs. 23.2% for the right unnumbered valves). As was indicated above, the large differences in Polydora incidence were not associated with differences in either growth or mortality. A similar conclusion was reported earlier by Medcof (1946).

Data Analysis

Average shell lengths of animals surviving in each group, and number of survivors, were plotted against time for the duration of the main experiment as is shown in Fig. 1. A

TABLE 1. Results of experiment to test effects of handling procedures.

Treatment	Holding Condition	Separated	Grouped	Totals
A. Mortality — Number of mussels dying during tests				
Undisturbed	Unnumbered	6	5	11
	Numbered	7	14	21
	Subtotal	13	19	32
Disturbed	Unnumbered	13	14	27
	Numbered	7	6	13
	Subtotal	20	20	40
Total		33	39	72

Treatment	Holding Condition	Separated	Grouped	Weighted averages
B. Growth — Average increase in shell-length of survivors (mm)				
Undisturbed	Unnumbered	14.4	13.8	14.1
	Numbered	13.0	11.5	12.3
Weighted average		13.7	12.3	13.0
Disturbed	Unnumbered	10.5	16.4	13.5
	numbered	11.7	14.9	13.3
Weighted average		11.2	15.5	13.3
Weighted average		12.4	13.8	13.2

distinct seasonality is evident, which showed marked similarities between bays. We therefore decided to divide production events between two main "seasons" of the year, from mid-May to mid-November, and from mid-November to mid-May, and which we have designated the "warmwater" and "coldwater" seasons, respectively. The general season-to-season variations were studied by conversion of the mortality and growth data to instantaneous rates (Ricker 1975). Mortality and growth rates within each "season" are expressed as the equivalent annual rate of change to avoid the confusion of different lengths of observation periods over different parts of the total experiment. The experiment thus provides data from four successive seasons as indicated on Fig. 1.

Growth observations of the individually identified mussels were classified within season into fast, average, and slow growths. That is, for each depth, location, and season, the instantaneous rate of growth of each surviving individual was plotted against its seasonal initial shell length and a polynomial fitted to the points. Additional polynomials were then calculated on either side of this average so as to effectively divide the total array of points into three approximately equal lots, which were termed the fast, average, and slow relative rates of growth. This arrangement permitted the establishment of a sequence of within-season relative growth rates for each animal. A series of two-way contingency tables was then set up for each experimental locality, in which the growth class of each individual in a given season was compared with its growth class in the next. Contingency tables for mussels which survived throughout the experiment were kept separate from those for animals dying before the experiment terminated. In analyzing data for animals that died, growth within the season when mortality occurred was not used. Tables constructed in this manner were initially subjected to standard χ^2 analyses. To check our impression of growth persistence along the main diagonal, the transect analysis of Doyle (1976) was used.

An additional method for determining the consistency of season-to-season growth rates was attempted since the data series provided information on each individual and we wished to extract any additional information from the data series that this treatment might have afforded. Accordingly, the growth data for each surviving individual were ranked in each season. Kendall and Spearman rank correlation coefficients (Kendall 1962) were then calculated between each of the four seasonal data sets. However, because individuals were of different sizes during the experiments and there was significant negative correlation of growth with size, ranking by growth rates alone would place constraints on the series, giving rise to falsely high values of ranking agreement. Accordingly, each seasonal growth observation was "normalized," using the polynomial to express the observed growth as growth relative to that of an average individual of the same shell size and experimental lot.

Instantaneous mortality rates were calculated by season for each growth lot and for each embayment, and the data analyzed by multiple regression techniques. This treatment was supplemented by probit analysis of the mortality observations. Because of low mortalities for the biweekly periods, accumulated mortality to the end of each 4-wk period was determined for each starting size-group. This was expressed as a percentage of the starting number at

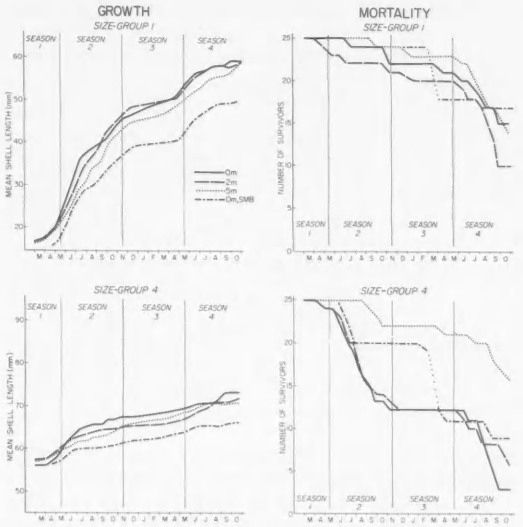

FIG. 1. Mean shell length increases and mortalities with time (season), location, and depth of size-groups 1 and 4 (0, 2, and 5 m are from Bedford Basin; SMB = St. Margaret's Bay).

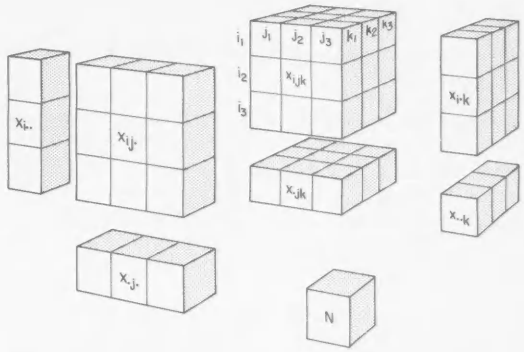

FIG. 2. Schematic arrangement of data for 3-dimensional analysis of seasonal individual growth rates. Throughout the analysis columns (j) are the first growing season and rows (i) the second growing season of consecutive "interseason" contingency tables. The depth (k) dimension is used to study other variables. Symbols in the various summation boxes are as used in Table 2 to calculate components of variance (information), following transformation of all entries to $x \ln x$, the Information Statistic (Kullback 1968).

the beginning of each experimental year. The cumulative percentage was plotted as the corresponding "probit" (Finney 1964) against time. The resulting data permitted the calculation of linear indices of mortality rates for comparisons between data groupings.

The components of variation contributing to the apparently nonrandom assortment of growth types were studied using the "Information Statistic" ($\sum x_i \ln x_i$) which, according to Kullback (1968), is asymptotically equivalent to the χ^2 test for large numbers and low to moderate class probabilities. In particular, we were interested in comparing the growth patterns revealed in the contingency tables for different periods of time, for different areas, and for different mortality "classes."

To carry out these essentially three-dimensional analyses, we sorted the 3×3 contingency tables comparing the frequency distribution of growth types in one season with that in the next season, into a series of three-dimensional boxes. That is, in all cases the rows (R) and columns (C) of the tables represent a particular interseason comparison while the third or depth (D) dimension is another experimental variable of interest. The entries in the body of the three-dimensional tables, corresponding to a given number of individuals in a row (i), column (j), or depth (k) classification, were then replaced by $x_{ijk} \ln x_{ijk}$, as were the corresponding marginal totals. The schematic arrangement of the tables is portrayed in Fig. 2 and the appropriate calculations are set out in Table 2.

The total variation (information) of the three-dimensional table is calculated (Kullback 1968) as:

$$2\Big(\sum\sum\sum x_{ijk} \ln x_{ijk} - \sum^{jk} x_{i..} \ln x_{i..} - \sum^{ik} x_{.j.} \ln x_{.j.} - \sum^{ij} x_{..k} \ln x_{..k} + 2N \ln N\Big)$$

where N is the total number of animals in the array. This calculation is shown in line 3 of Table 2. The total variation may be considered initially as consisting of two main components: a rows $\times$ columns ($R \times C$) part (line 1 of Table 2) and a row $\times$ column interaction with the depth dimension (R, C) $\times D$ (line 2 of Table 2). As is indicated in the table, in the information statistic calculation, these components are additive.

The interaction term of line 2 may itself be resolved into two additive components: a term measuring homogeneity along the depth (D) dimension, and a remainder which Kullback refers to as a "conditional rows $\times$ columns (R/C) interaction," that is, a rows $\times$ columns ($R \times C$) interaction with the (D) component removed. The corresponding calculations are shown, respectively, in lines 6, 4, and 5 in Table 2.

In similar fashion, the conditional (R/C) interaction is resolvable into two components which are a measure of the individual $R \times C$ table heterogeneities and a remainder, which is a basic between sample variation. The calculation is shown in lines 9, 7, and 8 of Table 2.

Since the information statistic is equivalent to χ^2 at the sample sizes employed here, the values calculated according to Table 2 may be tested by published χ^2 tables with the degrees of freedom calculated as shown in Table 2. The results of the analyses are discussed later from Tables 5 and 6. It may be noted that in Table 5 we analyze data for all animals which survived throughout the experiment. In Table 6 we analyze data for those that died during the experiments and compare tables for "nonsurvivors" with the parallel tables of survivors.

In a number of the contingency tables for a particular interseason comparison and area, particularly among the nonsurvivors, there were blanks among the entries. To allow us to carry out the calculations these zero values have been treated as "missing values." In all such cases we have followed the method of Davies (1963) of using the marginal totals to calculate a nonzero value which minimizes the

TABLE 2. Calculation of elements in a three-dimensional analysis of variance using the Information Statistic to approximate values of λ^2.

Line	Term	Calculation	df
1. Test of independence of row (R), column (C), and depth (D) classifications.			
1	$(R\times C)$	$2(\sum\sum x_{ij.} \ln x_{ij.} - \sum x_{i..} \ln x_{i..} - \sum x_{.j.} \ln x_{.j.} + N \ln N)$	$(R-1)(C-1)$
2	$D\times(R, C)$	$2(\sum\sum\sum x_{ijk} \ln x_{ijk} - \sum\sum x_{..k} \ln x_{..k} - \sum\sum x_{ij.} \ln x_{ij.} + N \ln N)$	$(D-1)(RC-1)$
3	$R\times C\times D$	$2(\sum\sum\sum x_{ijk} \ln x_{ijk} - \sum x_{i..} \ln x_{i..} - \sum x_{.j.} \ln x_{.j.} - \sum x_{..k} \ln x_{..k} + 2N \ln N)$	$(RCD-R-C-D+2)$
2. Test of independence of (D) components in $R\times C\times D$ tables.			
4	D-homogeneity	$2(\sum\sum x_{.jk} \ln x_{.jk} - \sum x_{.j.} \ln x_{.j.} - \sum x_{..k} \ln x_{..k} + N \ln N)$	$(D-1)(C-1)$
5	Conditional (R/C)	$2(\sum\sum\sum x_{ijk} \ln x_{ijk} - \sum\sum x_{.jk} \ln x_{.jk} - \sum\sum x_{ij.} \ln x_{ij.} + \sum x_{.j.} \ln x_{.j.})$	$C(D-1)(R-1)$
6	$D\times(R, C)$	from line 2	$(D-1)(RC-1)$
3. Test of homogeneity within $R\times C$ tables over various samples.			
7	(R, C)-homogeneity	$2(\sum\sum x_{i.k} \ln x_{i.k} - \sum x_{..k} \ln x_{..k} - \sum x_{i..} \ln x_{i..} + N \ln N)$	$(R-1)(D-1)$
8	(R, C, D) interaction	by difference	$(R-1)(C-1)(D-1)$
9	Conditional (R/C)	from line 5	$C(D-1)(R-1)$

sum of squares. The insertion of a missing value requires a reduction in the degrees of freedom. The use of missing values is signalled in Tables 5 and 6 by reductions in the degrees of freedom below that called for in the Table 2 calculations. In general, the substitution for zero values reduces the sensitivity of the tests.

Results

Overall Growth and Mortality Patterns

Cumulative growth and mortality curves were compiled separately for each size-group in each test situation. In Fig. 1 are given the results for the smallest and largest size-groups. They exhibit the usual extremes of the phenomena observed: relatively rapid growth and low mortality among small animals but slow growth and high mortality among the large. Inspection of the curves indicates other differences between size-groups and areas. For example, animals held at the surface in St. Margaret's Bay grew less than those held in Bedford Basin and showed lower mortality except for a period in March of the second growing year when several animals were damaged by ice. Mussels held in Bedford Basin grew to relatively larger sizes, but larger animals held near the surface showed pronounced mortalities during midsummer.

The cumulative curves for both small and large mussels clearly indicate the seasonal nature of the production processes. During much of the coldwater seasons (1 and 3) which run from mid-November to mid-May, the nighttime air temperatures are below freezing and from December through March there may be ice in the sea water and in the littoral zone. There is little growth at this time. However, the coldwater season also includes the period of the spring plankton bloom which in these waters occupies a 2–3-wk period which is generally completed before the end of April (Platt 1971). Figure 1 shows that growth appears to undergo a seasonal upsurge at the time of the plankton bloom but continues to rise beyond this, reaching a maximum around mid-May. The warmwater seasons (2 and 4), from mid-May to mid-November, span the annual spawning period for mussels from local waters. Figure 1 shows that growth continues at a gradually reducing rate throughout the warmwater seasons, except for a lesser growth surge in September–October in Bedford Basin at the time of a fall plankton bloom there.

Mortalities also show seasonal surges. They appear to be generally lowest during the coldwater months, rising gradually as the water warms, reaching a peak about August.

Because of the within-season variations and gradual transitions in productivity, any subdivision of the annual production processes is somewhat arbitrary. In what follows we frequently refer to average "seasonal" rates of growth and mortality which are calculated for these two fixed semiannual periods of the year.

Instantaneous Growth and Mortality Comparisons

For mussels held at the surface in Bedford Basin and St. Margaret's Bay, polynomial equations relating average instantaneous rates of growth to their seasonal initial shell lengths by season and area are drawn in Fig. 3. The curves indicate the general uniformity which might be expected of a common stock although the rate differences which led to the accumulated differences of Fig. 1 are evident. At intermediate shell sizes, St. Margaret's Bay appears to have supported generally slower growth than Bedford Basin, although small animals grew the most rapidly there during the coldwater seasons, and larger St. Margaret's Bay animals did relatively well during the warmwater season. It is of passing interest that in both St. Margaret's Bay and Bedford Basin the polynomial fits suggest that the smaller size-groups of mussels appeared to grow the faster during the coldwater season, that is, during the spring plankton bloom, while the larger mussels grew more rapidly in the "summer" or warmwater season. However, with the high scatter of points about the polynomial, the significance of any such pattern is ques-

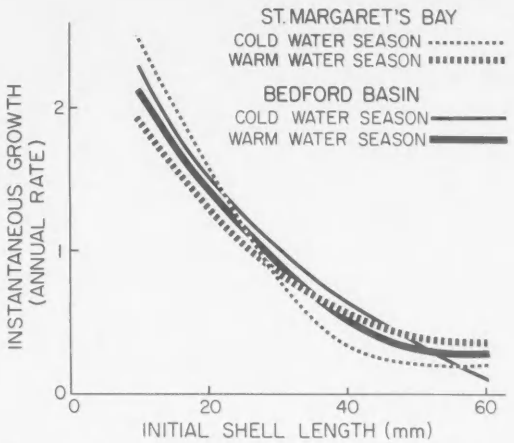

FIG. 3. Polynomial fits for growth of mussels during warm and cold water seasons in St. Margaret's Bay and Bedford Basin.

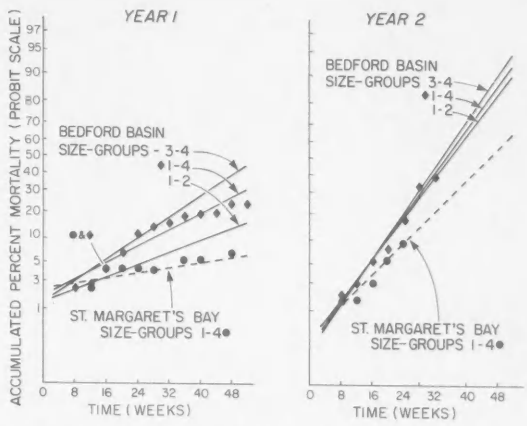

FIG. 4. Regression lines of the probit of mortality against time by area, size-group and year.

tionable. As may be inferred from Fig. 1, the growth rates at various depths within Bedford Basin did not show significant differences.

The major productivity differences among the experimental lots appear in the mortality rates, although with the small numbers involved in individual lots, it is not easy to make general statements about them. Within Bedford Basin mortality differences among depths were quite variable, hence data for the three depths were combined. From the resulting data set a series of 4-wk mortality rates was drawn up similar to Fig. 1. It showed a regularity of within-year mortality pattern which appeared to be related to shell length. Accordingly, Bedford Basin data from the two smaller size-groups were totalled separately from those of the two larger size-groups, and the annual mortality cycle constructed for the 20-mo experiment. Because of smaller numbers, the mortality series in St. Margaret's Bay was derived by summing over all size-groups.

Mortalities in each 4-wk period were expressed as accumulated percentages of the number at the beginning of each experimental year, and plotted as probits against time as shown in Fig. 4. From the slopes of the probit lines it is clear that in year 1 of the experiments the mortality rates were relatively low, although the data from Bedford Basin show that in that year the larger animals died faster, and both size-groups showed mortality rates higher than in St. Margaret's Bay. The principal feature of the series is the uniformly higher mortalities during the second experimental year. This higher mortality rate occurred in both areas and appeared to be independent of shell length (i.e. size-group at the beginning of the experiment).

The mortality may be studied in further detail in Fig. 5 where average instantaneous mortality rates for the two seasons are plotted by size and areas against corresponding initial shell lengths. In this form it is clear that exceptionally high mortalities were confined to the warmwater season in Bedford Basin and that during the warmwater season in both embayments the mortality rate seemed to increase with size. Mortality during the coldwater season was lower in Bedford Basin and appeared to affect all size-groups equally in both areas.

Given the relationships of both growth and mortality to shell length there is clearly an inverse relationship between them which is most marked in the warmwater seasons in Bedford Basin. A simple correlation analysis suggested that this inverse relationship may also characterize the St. Margaret's Bay data. However, the significance of the relationships is not easy to assess from the simple correlations. We therefore reexamined them using multiple regression. In a first analysis, seasonal instantaneous mortality as dependent variable was studied in relation to instantaneous growth and shell length, treated as independent variables, within each holding lot and season. The *F*-ratios for individual regressions indicated that relationships during the coldwater seasons in Bedford Basin and for all seasons in St. Margaret's Bay were not statistically significant so these data were eliminated from the analyses. The results for the warmwater seasons in Bedford Basin are summarized in Table 3.

All the data in the table show strong simple negative correlations between instantaneous warmseason mortality and growth, although in almost every case this relationship is weaker than is the correlation of either mortality or growth with shell length. The simple correlation of growth with length was consistently higher than -0.9. Under these circumstances it is hardly surprising that the multiple correlation shows that when the length variable is held constant the strong simple inverse relationship between mortality and growth disappears or even becomes positive. With the strong in-

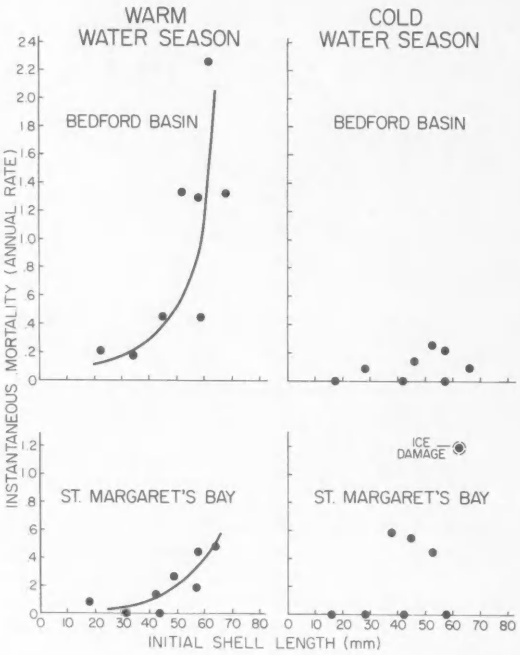

FIG. 5. Annual instantaneous mortality by location and season.

fluence of length it is inappropriate to include both growth and shell length as independent variables in the analysis.

With the results of the probit analyses in mind, the mortality study for the Bedford Basin data was revised. In this case mortality as dependent variable was related to "growth" and "season of growth" (i.e. 1st or 2nd growing season) as independent variables. The results are shown on the bottom line of the table. The *F*-ratio for the regression rose from 10.7 to 13.3 for this test. The results show that when season of growth is accounted for, there is a significant negative correlation between instantaneous mortality and growth rate. However, the season of growth appears as the strongest predictor of mortality. The partial regression coefficient indicates that irrespective of growth rate, mortalities in Bedford Basin during the second warmwater season were 50% higher than in the first warmwater season.

GROWTH AND MORTALITY PATTERNS AMONG INDIVIDUALS

The foregoing analyses show only small differences in growth rates among the experimental growth lots placed in the two embayments although the mortality differences suggest that total productivity differences of the areas may be relatively large. The relationship between growth and mortality rates warrants further examination, which is made possible by the data on growth and time of mortality of the individual mussels that were identified throughout the experiment.

As indicated under "Methods" the polynomial equations of individual growth rates versus initial shell length were used to classify the successive growth observations into fast, average or slow, and two-way contingency tables (3×3 cells) comparing frequencies of growth types from one season to the next were set up for each of the four experimental situations. Separate contingency tables were compiled for those animals which survived throughout the experiment, and for those which died during the experiments. Thus for each experimental situation we have three contingency tables for the survivors, comparing frequencies of growth types in seasons 1 and 2, 2 and 3, and 3 and 4, and two for nonsurvivors, comparing seasons 1 and 2, 2 and 3, for a total of twenty 3×3 tables of growth patterns.

For the initial analysis, tables of growth-type frequencies (for survivors and nonsurvivors separately) were summed over all interseasons to give a composite interseason pattern for each experimental situation. The resulting 3×3 tables were tested by χ^2 analysis for independence of the row $\times$ column classification (Table 4A). For all tables of survivors except the Bedford Basin 2-m group, the χ^2 values were significant at the 5% probability level, indicating that the overall classification of growth types was not independent from

TABLE 3. Statistics of multiple regression analyses of Bedford Basin data on growth (*g*), shell-length (*l*), mortality (*m*), and growing season (*s*) for the warmwater seasons.

	Simple correlations				Multiple regression coefficients				
	m with *g*	*m* with *l*	*g* with *l*	*F*-ratio	Intercept	*mg*·*l*	SD *mg*·*l*	*ml*·*g*	SD *ml*·*g*
0 m	−0.59	0.79	−0.95	21.53	−9.98	4.43	1.23	0.18	0.04
2 m	−0.84	0.87	−0.94	8.08	−0.33	−0.20	0.90	0.03	0.03
5 m	−0.49	0.49	−0.96	0.80	0.65	−0.58	2.00	1.08	0.08
0–5 m	−0.60	0.69	−0.95	10.69	−3.22	1.18	1.02	0.07	0.03
	m with *g*	*m* with *s*	*g* with *s*			*mg*·*s*		*ms*·*g*	
0–5 m	−0.60	0.72	−0.62	13.28	1.31	−0.51	0.37	0.49	0.16

TABLE 4. Analysis of 3 × 3 contingency tables of successive interseason individual growth rates for all seasons. A, χ^2 calculation (4 df); B, Transect analysis.

		Survivors	Nonsurvivors
A.	St. Margaret's Bay		
	0 m	21.6	3.4
	Bedford Basin		
	0 m	26.4	4.9
	2 m	3.2	8.1
	5 m	14.1	1.9
B.	St. Margaret's Bay		
	0 m	0.97±0.10	1.32±0.25
	Bedford Basin		
	0 m	1.53±0.14	1.28±0.17
	2 m	1.15±0.15	1.29±0.21
	5 m	1.31±0.11	1.21±0.18

one season to the next. Among the nonsurvivors data for only the Bedford Basin 2-m experiments showed significant χ^2 values. Overall mortalities in Bedford Basin 5 m, and St. Margaret's Bay, were relatively low, so that the result showing no measurable departure from random assortment in these cases was expected. The reason for the difference between survivors and nonsurvivors in the shallower holdings is examined in more detail later.

Inspection of the data in the eight tables indicated that there may be effects of seasonal change involved in the overall χ^2. That is, these composite tables consist of sums of successive warmseason, coldseason comparisons, or vice versa, in which there is a tendency towards overall acceleration or deceleration which may or may not be balanced in the sum. However, much of the nonrandom effect seemed to come from an aggregation of classifications along the main diagonal of the tables. Accordingly, the eight composite tables were subjected to an analysis of the main diagonal, by calculating the transect coefficient (Tr) of Doyle (1976) (Table 4B). Seven of the eight tables, including all of the tables for the nonsurvivors, showed a significant aggregation along the main diagonal, suggesting that in general a mussel with a relatively fast, average, or slow growth in one season tended to have a similar relative growth rate in the next.

The appearance of a significant consistency of growth rates within individuals taken from a single source stock is of sufficient importance to warrant closer scrutiny. The data used in the contingency tables were based on a classification scheme, which is clearly only one of a number of possible classification schemes. However, since all individuals used in the experiments were identified and measured at regular intervals, it is possible to eliminate some of the classification bias by ranking the individuals according to actual growth measurements. The possible source of bias arising through the linkage of growth rate with shell size and the wide selection of starting initial shell sizes was avoided by the "normalizing" procedure described earlier.

Kendall and Spearman rank correlation coefficients on the normalized data were calculated for all possible seasonal combinations for the mussels held at the surface in Bedford Basin and St. Margaret's Bay. Only animals which survived throughout the experiment were used. In all cases the correlations corresponding to the 3 × 3 contingency tables for successive seasonal comparisons in both Bedford Basin and St. Margaret's Bay were significant at the 5% probability level, and in all but one case were significant at the 0.1% probability level. Correlations for Kendall's τ ranged from 0.31 to 0.52 for 38 and 61 individuals, respectively. It is of further significance that rank correlations between nonconsecutive seasons were weaker, although correlations between rankings in the two warmwater seasons 2 and 4 were still significant at the 5% level. Correlation between rankings of the coldwater seasons 1 and 3 (0.25) was significant at the 5% level for Bedford Basin, but insignificant (0.11) in St. Margaret's Bay. Correlations between seasons 1 and 4 were very nearly the same as for seasons 1 and 3.

PATTERNS OF GROWTH BY SEASONS, AREAS, AND MORTALITY CLASSES

Confirmation by the χ^2 and rank correlation tests of highly significant growth patterning within individuals calls for further study of the pattern in relation to the other experimental variables. For this purpose we employed the information statistic, arranged in a series of additive components to provide an analysis of variance as outlined in Table 2. Results are shown in Tables 5 and 6.

The analyses of the growth data for the survivors in Table 5 are set out according to various classifications under headings. For example, the data under the first heading are the information statistic, degrees of freedom and probability levels for the St. Margaret's Bay experiment. Heading 2 denotes the Bedford Basin 0-m experiment, and so forth. We begin by examining the St. Margaret's Bay results in detail.

Under the St. Margaret's Bay heading the third (D) dimension of the set of 3 × 3 contingency tables compares the three successive interseason tables for seasons 1 and 2, 2 and 3, and 3 and 4. The ($R \times C$) calculation of line 1 is therefore the variance as reflected in the sum over the three interseasons and is equivalent to the initial χ^2 calculation reported for the St. Margaret's Bay data in Table 4A although Table 5 values are lower because of the correction for missing values in one of the component tables here. Together with the interaction term [$D \times (R, C)$] of line 2, it gives a measure of the total variance in line 3. In all three lines the calculated information (approximate χ^2) exceeds the tabled χ^2 value at the 1% probability level. It is to be noted, however, that the interaction term of line 2 is considerably larger than the $R \times C$ term of

TABLE 5. Three-dimensional analysis of variance (information) of individual growth rates of survivors using different measures along the third dimension. (Info. stat. = information statistic, asymptotically equivalent to χ^2; df = degrees of freedom; P = probability level * = <0.05, ** = <0.01, n.s. = >0.05.)

Heading no.	1			2			3			4			5			6								
Data set	St. Margaret's Bay			Bedford Basin — 0 m			Bedford Basin — 3 depths combined			Bedford Basin — 3 interseasons combined			Bedford Basin — all depths and St. Margaret's Bay all interseasons			Bedford Basin — all depths — and St. Margaret's Bay								
																Interseason 1–2			Interseason 2–3			Interseason 3–4		
Third dimension term	3 interseasons			3 interseasons			3 interseasons			3 depths			2 areas			2 areas								
Line term	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P
1 $R \times C$	15.9	4	**	21.2	4	**	30.3	4	**	30.3	4	**	31.0	4	**	13.6	4	**	15.7	4	**	9.3	4	n.s.
2 $D \times (R, C)$	118.1	10	**	40.8	12	**	85.2	15	**	25.6	16	n.s.	16.0	8	*	16.9	8	*	12.2	8	n.s.	36.5	8	**
3 $R \times C \times D$	134.0	14	**	62.0	16	**	115.5	19	**	55.9	20	**	47.0	12	**	30.5	12	**	27.9	12	**	45.8	12	**
4 D-homogeneity	75.3	4	**	16.2	4	**	32.1	4	**	4.5	4	n.s.	0.5	2	n.s.	9.1	2	*	6.8	2	*	8.1	2	*
5 Conditional (R/C)	42.8	6	**	24.6	8	**	53.1	11	**	21.1	12	*	15.5	6	*	7.8	6	n.s.	5.4	6	n.s.	28.4	6	**
6 $D \times (R, C)$	118.1	10	**	40.8	12	**	85.2	15	**	25.6	16	n.s.	16.0	8	**	16.9	8	*	12.2	8	n.s.	36.5	8	**
7 (R, C)-homogeneity	38.2	4	**	23.2	4	**	46.5	4	**	15.0	4	**	0.2	2	n.s.	5.1	2	n.s.	5.6	2	n.s.	12.2	2	**
8 $(R, C, D,)$ interaction	4.6	2	n.s.	1.4	4	n.s.	6.6	7	n.s.	6.1	8	n.s.	15.3	4	**	2.7	4	n.s.	0.2	4	n.s.	16.2	4	**
9 Conditional (R/C)	42.8	6	**	24.6	8	**	53.1	11	**	21.1	12	n.s.	15.5	6	*	7.8	6	n.s.	5.4	6	n.s.	28.4	6	**

TABLE 6. Three-dimensional analysis of variance (information) of individual growth rates of nonsurvivors, and comparison of survivors and nonsurvivors. (P level as for Table 5.)

Heading no.		1	2			3			4			5		
Data set		St. Margaret's Bay	Bedford Basin — 3 depths combined			St. Margaret's Bay 2 interseasons combined			Bedford Basin depths and 2 interseasons combined			Bedford Basin and St. Margaret's Bay — all data for nonsurvivors		
Third dimension term		2 interseasons	2 interseasons			Survivors vs. nonsurvivors			Survivors vs. nonsurvivors			2 areas		
	Line term		Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P	Info. stat.	df	P
1	$R\times C$		9.3	4	n.s.	19.5	4	**	20.5	4	**	8.2	4	n.s.
2	$D\times(R, C)$		30.5	7	**	8.2	7	n.s.	8.5	8	n.s.	6.2	7	n.s.
3	$R\times C\times D$	Insufficient data	39.8	11	**	27.7	11	**	29.0	12	**	14.4	11	n.s.
4	D-homogeneity		3.5	2	n.s.	0.3	2	n.s.	3.0	2	n.s.	1.0	2	n.s.
5	Conditional (R/C)		27.0	5	**	7.9	5	n.s.	5.5	6	n.s.	5.2	5	n.s.
6	$D\times(R, C)$		30.5	7	**	8.2	7	n.s.	8.5	8	n.s.	6.2	7	n.s.
7	(R, C)-homogeneity		28.9	2	**	0.6	2	n.s.	2.8	2	n.s.	1.4	2	n.s.
8	(R, C, D) interact.		−1.9	3	n.s.	7.3	3	n.s.	2.7	4	n.s.	3.8	3	n.s.
9	Conditional (R/C)		27.0	5	**	7.9	5	n.s.	5.5	6	n.s.	5.2	5	n.s.

line 1, from which it appears that our earlier assessment of heterogeneity in Table 4A was correct in ascribing part of the variance to the influence of the seasonal growth differences.

The interaction term is analyzed into components in lines 4 and 5. The D-homogeneity term of line 4 exceeds the 1% probability level, verifying the heterogeneity between successive interseasonal comparisons. However, the conditional (R/C) interaction in line 5 is also large, helping to verify that the heterogeneity detected in line 1 did indeed result from within interseason growth $(R \times C)$ classifications, a conclusion which was also clear from the rank correlation tests. The further analysis of this conditional (R/C) interaction (i.e. heterogeneity within the individual contingency tables for different interseason comparisons) is shown in lines 7 and 8. Apparently, only a small and insignificant fraction of the conditional (R/C) interaction can be attributed to a basic "sampling" error.

The results for the Bedford Basin 0-m experiment under the second heading of Table 5 are very like those for St. Margaret's Bay, although the importance of successive interseason comparisons (line 4) appears to be somewhat less.

Under the third heading, the data for all three holding depths in Bedford Basin are combined. The results are similar to the surface experiment suggesting that there was no important effect of depth on the growth patterning. This conclusion is confirmed under heading 4 where the Bedford Basin data have been aggregated over interseasons and the D-dimension of the analysis consists of a direct comparison of the data by depths. The third dimension has an insignificant effect on the total variance, suggesting that the different result for the 2-m holding in Table 4A was fortuitous.

The results under heading 4, comparing the depths of holding, provide interesting confirmation of the previous analyses. That is, the significant total heterogeneity (line 3) appears in the overall $(R \times C)$ table (line 1). The interaction term (line 2) does not show significant effects, although when it is analyzed into components (lines 4 and 5) it is seen that the D component representing different depths is insignificant while the remaining conditional (R/C) term, in keeping with the high value in line 1, exceeds the χ^2 value at the 5% level. When this interaction term is again resolved into components it appears in line 7 that the (R/C) heterogeneity is highly significant when the successive interseason effects are accounted for entirely. That is, the test confirms that the high variance is associated with the growth rate persistence from one season to the next.

Under heading 5 we have combined data over all seasons and depths for a comparison of the St. Margaret's Bay data with those of Bedford Basin. While the results in lines 1 and 5 continue to signal the existence of significant heterogeneity within the $R \times C$ contingency tables, the low or insignificant values in lines 2 and 4 suggest that the heterogeneity is not attributable to differences between growing areas. In this case, however, the interaction term of line 8 is highly significant suggesting that in the compilation of the tables we have attempted to group elements that are too diverse, throwing suspicion on the entire result. Accordingly, we have repeated this analysis, using data

from each of the interseasons separately to compare the two growing areas. The results under heading 6 for interseasons 1 to 2 and 2 to 3 now show that while the $(R \times C)$ heterogeneity is significant, the major part of the variance is due to the difference between areas. By contrast, for interseason 3 to 4 the high value of the interaction term of line 8 again signals the use of diverse elements as under heading 5. Inspection of the original data shows that in this interseason a disproportionately large fraction of Bedford Basin animals were classified as slow growers, and that this difference overrode all other effects.

As is evident in Table 6, study of the growth patterning of the animals which did not survive to the end of the experiments is limited by the small numbers involved. For example, the contingency table for the St. Margaret's Bay holding for interseason 2 to 3 contained only 9 animals, all of which were in three of the possible 3×3 categories. For this reason it is not possible under heading 1 to study the interseason growth differences among the St. Margaret's Bay nonsurvivors, in parallel with the first heading of Table 5. However, the larger numbers held in Bedford Basin, together with the higher mortalities there, permit a study of growth patterning among them. The results under heading 2 are slightly different from those of the survivors. That is, the high total heterogeneity of line 3 appears to be entirely due to the D interaction with the $(R \times C)$ classification (line 2); the overall $R \times C$ classification itself (line 1), in keeping with results in Table 4A (0 m), does not demonstrate significant heterogeneity. Lines 4 and 5 show, however, that this high interaction term is not a result of the interseason component, and line 7 confirms that the heterogeneity of the (R/C) classification shows up if the interseason dimension is accounted for. Apparently the Bedford Basin nonsurvivors show the same basic growth patterning that characterizes the survivors, but this was obscured in the summary table (line 1) by "compensatory" distributions (i.e. accelerations and decelerations of growth) in the successive interseasons. This interpretation is confirmed by data under the next two headings, 3 and 4, which compare overall interseason contingency tables for survivors and nonsurvivors in each of the two experimental localities. In both cases the results in lines 2 and 4 fail to demonstrate any differences in growth patterns between the animals which died during experiments and those that survived throughout.

Finally, under heading No. 5 we compare the growth patterns among the nonsurvivors held in St. Margaret's Bay and Bedford Basin. In this instance none of the tests reveal departures from a homogeneous distribution. That is, the major differences in numbers dying between the two bays do not appear to have selectively affected the different growth rate "strains" involved. However, the low numbers available for this test do not suggest that the conclusion has a strong basis. It must in fact be viewed with considerable caution in view of the results in Table 5 for the survivors. Characterization of the growth types among the dying animals appears to require experiments with larger numbers than we used here.

Discussion

Cumulative growth and mortality curves for mussels from the single source stock indicate differences between the two bays over the 20-mo holding period. Though surprisingly small, such growth rate differences were anticipated on the basis of known dissimilarities in both the topography and dynamics of the embayments (MacKinnon and Mann 1973) as well as in the timing and vertical distribution of the primary productivity (Platt 1975). We have little prior knowledge of the effects of geography on mortalities. The cumulative mortality curves suggest that net productivity differences between the bays are greater than would be reflected in the gross productivity measurements of growth alone. On the basis of our results it appears, therefore, that both growth and mortality measurements should be utilized in environmental indexing.

Detailed examination of the growth and mortality rates within arbitrary semiannual seasons provided a more sensitive index of similarities and differences between embayments than was available from the aggregated results. Growth rates declined sharply with shell size in both areas and differed slightly between seasons, but the data suggest that the cumulative result depended somewhat on initial shell size of the test lots. Mortality patterns in the two areas showed fewer parallels. Mortality was generally low in the coldwater seasons in both areas but distinctively high in the warmwater seasons in Bedford Basin, where there was also a strong dependence on size. The principal feature of the mussel mortality was the marked rate of increase in the second experimental year in both bays. In Bedford Basin mortality rate increased between two and three times, depending on size. In St. Margaret's Bay mortalities were generally lower and size effects could not be measured but mortality in the second year increased over fivefold. With the strong differences in mortality rates between first and second growing season and the possible size dependence of both growth and mortality, it is clear that differences in the cumulative growth and mortality curves or in net productivity calculations between bays may be as much a result of the distribution of production processes and size-groups between the seasons as it is a result of differences in the areas themselves. Environmental indexing using mussels clearly requires careful experimental design.

The assessment index is further complicated by the observed growth persistence within individuals, which is reminiscent of genetically controlled growth rates. This is consistent with the evidence of Levinton and Koehn (1976) that *Mytilus edulis* populations generally possess a large amount of genetic variability and of Innes and Haley (1977) that a substantial amount of phenotypic growth variation in young mussels is evidently of genetic origin.

From our experiments it was clear that classification of the samples among growth-rate classes was affected

by interseason sequences. However, when the effect of different seasonal sequences was eliminated, the evidence for a possible genetically based persistence within growth classes was enhanced and appeared to explain an important part of the total growth variance in the experiments.

It is of considerable importance to the potential of mussels as environmental indexing organisms that the difference in mortality rates between bays apparently showed significant interaction with the growth types within the stock. That is, the presence of different growth genotypes appeared to affect the productivity comparison between bays. Moreover, the evidence of interaction of both growth and mortality with body size would imply that appreciation of environmental differences using mussels would be affected by the initial proportions of the growth types in the source stock.

Levins (1968) has suggested that populations may generally be comprised of a range of genotypes, each of which is suited to a specific environment, as an adaptation to fluctuating environments. The possible appearance of growth types of *Mytilus edulis* within the single source stock may be related to such adaptation, raising the question of whether a different cohort from the same area might have given a different appreciation of the productivity difference between the test environments, or conversely, whether the apparent area difference is in part a temporal difference. In fact, the high mortality of mussels in their second year, while reminiscent of mortality patterns found by Milkman and Koehn (1977), may have reflected a sensitivity of the given stock configuration to environmental events which were on a large enough scale to have affected the two neighboring bays in which experiments were conducted.

We conclude that an environmental index using growth and mortality rates of *Mytilus edulis* may well provide a sensitive measure of relative productivity between areas. However, it is clear that such an index can be significantly affected by all those factors of which we might have had a priori suspicions: genetic mix of growth types, size dependence of production parameters, and interactions arising from the distribution of growth types and body sizes within and between seasons or production years. With requisite care in experimental design, these factors would not adversely affect the development of a repeatable index. However, two questions remain. First, our data revealed major differences in mortality rates between areas, but it is not possible from our information to rule out a relationship between mortality and physiological properties which may be under genetic control. Any genetic differences in mortality rates could evidently bias the area comparisons more than the growth effects. Second, we have no way at present to link our direct measures of production parameters with the physiological mechanisms which may underlie them. Bayne et al. (1977) have outlined and tested means of capitalizing on direct physiological measures as comparative ecological indices. The two systems of indices are potentially complementary, although one or the other may offer different advantages in different situations. It is our expectation that further field studies, planned in association with physiological measurements, should resolve these remaining questions.

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Terrigenous Organic Matter in Sediments of the St. Lawrence Estuary and the Saguenay Fjord[1]

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POCKLINGTON, R., AND J. D. LEONARD. 1979. Terrigenous organic matter in sediments of the St. Lawrence Estuary and the Saguenay Fjord. J. Fish. Res. Board Can. 36: 1250–1255.

The proportion of land-derived organic matter in sediments of the upper St. Lawrence Estuary is unexpectedly low. In the Saguenay Fjord and the lower estuary, high organic carbon to nitrogen ratios and the presence of lignin indicate a substantial contribution of organic matter from terrestrial sources. The proportion of terrigenous organic matter decreases rapidly thereafter, approaching levels typical of marine sediments in the open Gulf.

Key words: Organic matter, sediments, carbon to nitrogen ratio, lignin, St. Lawrence Estuary, Saguenay Fjord

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La proportion de matière organique d'origine terrestre dans les sédiments de l'estuaire moyen du Saint-Laurent est faible, tandis que dans le fjord du Saguenay et dans l'estuaire maritime, de fortes proportions de C par rapport à N et la présence de lignine indiquent une grande contribution de source terrestre. La quantité de matière organique terrigène décroît par la suite, pour atteindre des niveaux typiquement maritimes dans le haut du golfe Saint-Laurent.

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THIS work is part of a continuing study on sources and sinks of organic matter in the Gulf of St. Lawrence and adjacent waters (Pocklington 1976). The purpose of the present study is to interpret chemical analyses of surficial sediments in the St. Lawrence Estuary and the Saguenay Fjord in terms of the contribution of land-derived organic matter to the sediments. Measuring organic matter contained in sediments is of great biological importance. The determination of the quantity and quality of organic substances in sediments provides information as to the nutritional value of the substrates, an important factor in the estuarine environment.

The fate of river-borne organic matter, both dissolved and particulate, when it reaches the high salinity, high pH environment of estuaries, is currently in dispute (reviewed by Duce and Duursma 1977). Flocculation of terrigenous organic matter is accepted as an effective scavenging mechanism for the removal from the water column and transfer to the sediments of metals and organic compounds of both natural and anthropogenic origin (Ehrhardt 1977) but the extent is unknown. Experimental work suggests that in estuaries only 3–11% of riverine organic matter is flocculated (Sholkovitz 1976) but other studies show that increasing salinity results in rapid precipitation of the major fraction of terrigenous organic matter (Sieburth and Jensen 1968). Handa (1977) recommended that the extent and salinity dependence of the removal of organic matter from rivers in estuaries be established, and that a search for those organic compounds in marine sediments which represent land-derived organic matter should be conducted to determine how far riverine organic matter penetrates estuaries and what fraction exists in coastal and marine sediments. One of the recommendations of the NATO symposium on concepts in marine organic chemistry was to study the processes acting upon organic material in river water as it passes through the estuarine zone and the extent of removal during this passage (Anon. 1977).

[1]Bedford Institute of Oceanography Contribution.

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Methods

Marine sediments containing terrigenous organic matter can be identified by a combination of high organic carbon concentration, high organic carbon relative to nitrogen, and the presence of lignin (Pocklington 1976). Up to 30% of the weight of vascular land plants is lignin (Manskaya and Drozdova 1968). It is resistant to biodegradation, especially under anaerobic conditions (Dugan 1972), and has been found histologically intact in ancient marine sediments (Leo and Barghoorn 1970). Lignin is among the most stable of all organic compounds, particularly when complexed with amino acids in "humic" substances (Allison 1973). It is an unequivocal indicator of terrigenous organic

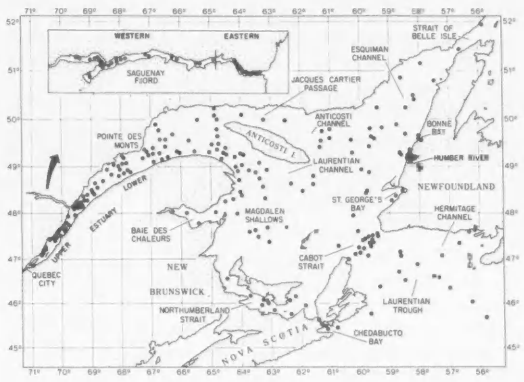

FIG. 1. Sample locations in, and nomenclature of, the Gulf of St. Lawrence and adjacent waters. Division into upper and lower estuary is at the Saguenay which is divided at 70°W into western and eastern basins by a sill.

matter (Pocklington and Roy 1975) being absent from marine biota (Lieth and Whittaker 1975). Organic carbon to nitrogen ratios have also been used as indicators of terrigenous addition to marine sediments based on an observed enrichment of carbon over nitrogen atoms in terrestrial (C:N atomic $\geq$ 12, Kukal 1971), as compared to marine (C:N atomic $\leq$ 10, Parsons 1975) organic matter. Among the first to use the C:N ratio was Trask (1955) whose average for surface samples off S. California was 8.0 (by weight). The median weight ratio in surface sediments of the Atlantic continental margin is 7.0 (Emery and Uchupi 1972: 371–373). In contrast, lignin has a C:N ratio of 1500 (Greaves and Schwartz 1952).

A sample of surface sediment was taken with a bottom grab at the locations shown in Fig. 1; water samples were taken at the same stations. Sediment color and gross texture were recorded at the time.

Organic analyses of the sediments of the Gulf of St. Lawrence by Loring and Nota (1973) were confined to "readily oxidizable organic matter" and provided no information on nitrogen. We determined both organic carbon and nitrogen using a commercial instrument (Hewlett-Packard 185B CHN Analyzer) calibrated with acetanilide, a standard which closely approximates the C:N ratio of marine organic matter, by the most-recently recommended procedures (Byers et al. 1978; Gibbs 1977). When X-ray diffraction indicated the presence of significant carbonate, the samples were treated with acid to remove this interference (Pocklington and Hagell 1975). In this study calcareous sediments were confined to the central Laurentian Channel east of Pointe des Monts.

A rapid semiquantitative test for lignin was conducted on all sediments (Pocklington and Hardstaff 1974) and a quantitative determination performed on lignin-containing samples (Pocklington and MacGregor 1973).

Results

Complete analytical results are given in Pocklington and Morash (1979) and summarized in Tables 1 and 2 and Fig. 2. Our set of over 200 samples, representative

TABLE 1. Organic carbon, nitrogen, and their ratios in the major sediment types of the Gulf of St. Lawrence.

		Gulf pelites[a]	Gulf sands[b]	Fjord[c] pelites
No. of samples		108	64	31
C_{org} (mg/g)	Mean[d]	16.5	4.9	25.1
	C_v%[e]	2.9	39.6	9.2
N_{org} (mg/g)	$\bar{x}$	1.92	0.62	1.55
	C_v%	5.4	51.6	11.0
C:N (atoms)	$\bar{x}$	10.1	10.7	18.9
	C_v%	2.4	2.6	5.6

[a]Material smaller than 0.05 mm, includes sandy pelites (up to 30% sand).

[b]Particle diameters between 2 and 0.05 mm, includes pelitic sands (up to 30% pelite).

[c]The Saguenay and Humber rivers are, in the regions sampled, fjords i.e. deep-basin, highly stratified, positive estuaries.

[d]All means are geometric.

[e]Coefficient of variation = standard deviation/mean × 100.

of all regions within the Gulf of St. Lawrence, shows organic carbon and nitrogen in the surface sediments to be lognormally distributed. Organic matter is related to sediment texture (Table 1). Of the two major classes of sediment in the Gulf, pelites (muds) have a significantly higher and less variable organic carbon and nitrogen concentration than sands. Pelites in the Saguenay and Humber fjords have higher and more variable organic carbon content than pelites elsewhere but lower and more variable nitrogen. The concentration of organic nitrogen is highest in pelites in the Gulf and lowest in sands, particularly those farthest from the ocean (correlation between organic nitrogen and longitude of sample location, $r = -0.51$, $n = 204$, $P < 0.01$). These general results confirm the well-known association of organic richness with sediment fineness (Bordovskiy 1965).

The ratio of organic carbon to nitrogen ranges from 5 to 50. The percentage of terrigenous organic matter in a sediment of our sample set is defined as 100 (log C:N − log 5). The mean for Gulf pelites though lower than, is not statistically significantly different from, that for Gulf sands; there is no difference in variability. High C:N ratios are limited to bays and fjords: the highest are found in the sediments at the head of the Saguenay and Humber fjords where there is a significant contribution from terrestrial vegetation (correlation between C:N and lignin $r = 0.31$, $n = 103$, $P < 0.01$). The C:N ratio shows little association with the sediment size description. The causes of variation in C:N ratio are due to the nature of the organic matter rather than the type of sediment.

To highlight changes in the quantity and quality of organic matter in the surface sediments from the St. Lawrence River to the open Gulf, the region was separated into defined areas (Table 2).

TABLE 2. Organic carbon and C:N ratio in the major sediment types of defined areas of the Gulf of St. Lawrence.

	Upper Estuary										
	Sands			Saguenay Fjord		Lower Estuary		Open Gulf[a]		Outside Gulf[b]	
	True sands	Pelitic sands	Pelites	Sands	Pelites	Sands	Pelites	Sands	Pelites	Sands	Pelites
n	9	7	9	14	22	7	33	6	30	10	18
C_{org}(mg/g)	1.0	7.4	18.2	4.2	25.7	4.1	14.8	7.3	13.6	4.6	21.9
C_g%	35	15	42	54	20	41	15	30	19	39	24
n	16		9	13	22	7	33	6	30	10	18
C:N (atoms)	10.2		13.6	15.3	21.1	13.8	12.7	11.2	9.2	9.1	8.5
C_g%	29		11	30	28	8	15	34	25	23	16
% terrigenous	3–49		38–50	18–63	49–93	38–47	18–52	9–48	12–44	8–37	14–34

[a]North of 48°N, west of 62°W, excluding Chaleur Trough and Jacques Cartier Passage.
[b]Laurentian Trough outside Cabot Strait.

SAGUENAY FJORD

The distribution of organic carbon in surface sediments of the Saguenay Fjord is bimodal (Fig. 2): the higher mode corresponds to the Western Basin which is predominantly pelitic and the lower to the Eastern Basin which is primarily sandy and not so conducive to the deposition of fine sediments containing much organic matter. Nearly all the organic matter has a high C:N ratio. The mean in the Western Basin is the greater but even in the Eastern Basin where the organic content is considerably lower, the C:N ratio still remains high compared to outside the fjord. The presence of identifiable lignin throughout confirms that the organic material is dominated by woody debris in areas of both high and low deposition.

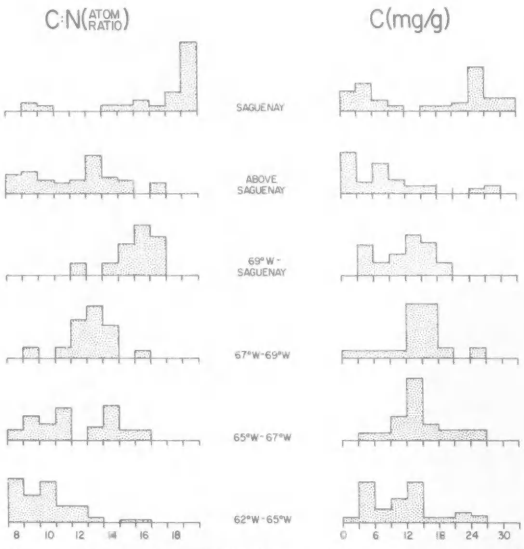

FIG. 2. Frequency distributions of organic carbon and C:N ratio by area.

The sands in the Saguenay Fjord have the same concentration of organic matter in them as sands in the lower estuary, but the pelites are among the most highly organic sediments in the Gulf (exceeded only by pelites in the Humber Fjord). The C:N ratio in fjord pelites is significantly higher than the ratio in the sands though the C:N ratio in the sands of the fjord is significantly higher than that in the sands of the upper estuary or the sands and pelites of the lower estuary. High C:N ratios throughout the fjord indicate that the major organic contribution is terrigenous.

UPPER ESTUARY

The sediments of the upper estuary (above the Saguenay) deserve detailed attention for it is here that the greatest amount of terrigenous influence might be expected. It is the only area in which the nonpelitic fraction dominates: true sands and pelitic sands each constitute one-third of the samples taken. The organic content of the true sands is the lowest of any class of sediments considered in this study. The mean C:N is low; <50% of the organic matter in upper estuary sands and pelitic sands is terrigenous. The pelites, in contrast, are more organic than pelites from the lower estuary and the open Gulf, and are the most homogenous in composition of all in this sediment size-class. There is a statistically significant difference between the composition of the organic fraction in the sands and the pelites of the upper estuary, but no significant difference exists between upper estuary and lower estuary pelites, both of which contain the same type of organic matter. The upper estuary and Saguenay Fjord sediments are unusual in that the pelites, rather than the sands, have more terrigenous material.

In the upper estuary the mean C:N ratio is lower than anywhere west of Pointe des Monts. Organic matter in the sediments of the area is not derived to an overwhelming extent from terrestrial sources; one half must come from the production of marine organisms. Much of this is brought into the upper estuary by the

tidal cycle (d'Anglejan and Ingram 1976). A turbidity maximum, maintained by tidal currents and flocculation, dominates the upper estuary within which preferential deposition of organic particulate matter occurs (Kranck 1979). In the comparable case of inorganic suspended material, only minor quantities from the St. Lawrence River accumulate in the upper estuary at the present time (d'Anglejan and Brisebois 1978).

Lower Estuary

In the lower estuary from the Saguenay to 69°W, the mean C:N ratio (14.4) is a little below that of the Eastern Basin of the Saguenay (14.9), but significantly higher than the mean ratio in the upper estuary (11.4) and further east (69°W–67°W) in the lower estuary (11.7). The source of much of the sedimentary organic matter in this part of the St. Lawrence Estuary is the Saguenay Fjord; this was implied by Loring (1975) and Loring and Bewers (1978) who found that the sediments of the fjord and the lower estuary were enriched with mercury and that terrigenous organic matter, specifically the lignin fraction, is the major carrier of mercury out of the fjord into the estuary. Their interpretation is confirmed by the evidence of the C:N ratios.

In the lower estuary as a whole (Saguenay to 67°W) the normal pattern of higher C:N in sands than pelites is established though the difference is not great. There is a highly significant difference between C:N in lower estuary pelites and C:N in open Gulf pelites, but no significant difference in concentration of organic matter. The C:N ratio in sands of the open Gulf is higher than that in the pelites but the difference is not statistically significant. There is also no significant difference between C:N in pelites inside and outside the Gulf in spite of the fact that there is generally more organic matter outside the Gulf.

Through the lower estuary to outside the Gulf the mean C:N ratio decreases regularly. We interpret this as a gradual decrease in the terrigenous contribution to the sediments. East of Pointe des Monts, the distribution of C:N ratios (Fig. 2) shows two major influences: lower ratios fall within the gyre west of Anticosti and higher ratios within the Gaspé Current system. In this region, C:N is significantly inversely correlated with the salinity of the bottom water ($r = -0.86$, $n = 17$, $P < 0.01$). The Gaspé Current is characterized by low salinity water which extends to the bottom. Higher C:N ratios are found in sediments below the less-saline water. The two sources of organic material in the sediments of this region are primary production in the open Gulf, known to be enhanced in the gyre W. of Anticosti, and terrigenous material from the estuary. Further to the south and east (65°W–62°W) higher C:N ratios virtually disappear and the mean approaches that of sediments outside the Gulf. There are few individual values which can be identified with terrigenous organic matter and these are all in the region of the Gaspé Current.

Discussion

Our results show that surface sediments in the Saguenay Fjord and in the lower estuary immediately outside the fjord contain a large contribution from terrigenous organic matter, that the small amount of organic matter in the sediments of the upper estuary is not predominantly terrigenous, and that there is a decreasing proportion of terrigenous organic matter in the surface sediments through the remainder of the lower estuary to the open Gulf.

Tan and Strain (1979) have used the ratio of ^{13}C to ^{12}C in the organic matter of surface deposits to examine the relative contributions of terrigenous and marine organic carbon to sediments in the Gulf of St. Lawrence. Their results confirm our own except in the upper estuary where they conclude that the organic matter in the sediments is entirely of terrestrial origin. Their sample is small ($n = 6$) and with exception of one sample taken S of I. d'Orleans comes only from the N. channel of the estuary which contains relict material from nearby recessional moraines (d'Anglejan and Brisebois 1978) that is probably unrepresentative of present-day depositional conditions. The suspended load from the St. Lawrence River is not deposited there but along the S. shore, when it is not transported out of the upper estuary altogether.

Tan and Strain (1979) attempted to quantify terrigenous vs. marine organic carbon using a material balance equation:

$$f_t = \frac{\delta_t - \delta_m}{\delta_t - \delta_m}$$

where f_t = the fraction of contributions of terrestrial organic carbon,
δ_t = $\delta^{13}C$ of organic carbon in sediment sample,
δ_m = $\delta^{13}C$ of marine organic carbon,
δ_t = $\delta^{13}C$ of terrestrial organic carbon (the $^{13}C/^{12}C$ ratio is expressed in $\delta^{13}C$ notation as defined by Craig [1957]).

Difficulty arises with the $\delta^{13}C$ values to be entered in the equation for the terrestrial and marine organic "end-members" (extreme components). Although dissolved inorganic carbon, the major carbon source for phytoplankton, has a $^{13}C/^{12}C$ ratio which is constant within 2‰ in surface seawater (Kroopnick 1974), the organic matter in seawater shows variations over a range of 10‰ (Craig 1953). Attached algae have $\delta^{13}C$ values of −12 to −23‰ (Haines 1976) and marine fauna an average $\delta^{13}C$ of about −15‰ so the marine "end-member," assumed but not determined by Tan and Strain (1979), is highly dependent upon species composition. The relative amounts of, for example, green algae ($\delta^{13}C = -22$‰) and blue-green algae ($\delta^{13}C = -15$‰) influence the $\delta^{13}C$ of oceanic plankton samples (Fontugne and Duplessy 1978).

Similarly the terrestrial "end-member," if entirely North American woodland, an almost exclusively C_3 plant regime (Tieszen 1978) should average −26.5‰

but introduction of a C_4 plant component from cultivated fields (C_4 plants include several cultigens of economic importance, for example, corn) would move the mean $\delta^{13}C$ toward higher values (about −12.5‰, Van der Merwe and Vogel 1978). Marine angiosperms have $\delta^{13}C$ values ranging from −3.0 to −13.9‰ (Fry et al. 1977) and could influence inshore $\delta^{13}C$ means. As Tan and Strain (1979) did not determine their terrestrial "end-member" either, the differences they found for example between mean $\delta^{13}C$ from the western basin of the Saguenay Fjord and the upper estuary could well reflect the difference between a fjord surrounded by forest and an estuary bounded by cultivated fields.

If we enter the calculations of Tan and Strain (1979) with the marine and terrestrial "end-members" of Sackett and Thompson (1963, as quoted by Tan and Strain 1979) rather than the ones chosen, the Saguenay Fjord sediments are reduced from 100 to 86% terrestrial and the lower estuary sediments raised from 7.5 to 35% terrestrial, which are much closer to our estimates. We conclude that the attempt to quantify terrestrial vs. marine contributions through carbon isotope ratios, in the absence of $\delta^{13}C$ determinations on likely "end-members," is premature.

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A Rapid Method for the Estimation of, and Some Factors Affecting, Copepod Production Rates in the Burlington Canal

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BORGMANN, U., C. LOVERIDGE, AND R. COVE. 1979. A rapid method for the estimation of, and some factors affecting, copepod production rates in the Burlington Canal. J. Fish. Res. Board Can. 36: 1256–1264.

A method is described for estimating in situ biomass production rates of copepods. The youngest naupliar stages are isolated by filtration through two different size sieves, and growth is measured after laboratory incubation by filtering through a series of eight filters. Since the filters appear to be relatively efficient at separating copepods of different sizes, copepod size can be estimated from the pore size of the filters alone, resulting in a very rapid procedure for calculating biomass. This method allows experimental manipulation of environmental conditions, permitting for example, an estimation of the relative importance of temperature and food abundance in the seasonal growth cycles of these organisms. It was concluded that, in the Burlington Canal, temperature exerts a greater influence on growth rate than does food concentration, although adaptation to food levels may be expressed indirectly, due to a similarity in the seasonal cycles for temperature and food. The method is also useful in predicting the potential impact of toxic substances on copepod production rates under natural conditions.

Key words: copepods, zooplankton, biomass production, temperature, food concentration

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On décrit dans cet article une méthode d'estimation in situ des taux de production de la biomasse de copépodes. Les plus jeunes nauplii sont isolés par filtration à travers des tamis de deux grosseurs différentes, et on mesure la croissance après incubation en laboratoire par passage à travers une série de huit filtres. Comme les filtres semblent séparer assez facilement les copépodes de différentes grosseurs, on peut estimer la taille de ces derniers par la grosseur des pores des filtres seulement, ce qui permet de calculer très rapidement la biomasse. Grâce à cette méthode, on peut manipuler expérimentalement les conditions de l'environnement, ce qui permet par exemple d'estimer l'importance relative de la température et de l'abondance de nourriture dans les cycles de croissance saisonniers de ces organismes. Nous concluons que dans le canal de Burlington, la température exerce sur le rythme de croissance une influence plus grande que la concentration des aliments, bien que l'adaptation à des niveaux d'abondance de nourriture puisse être exprimée indirectement, à cause d'une ressemblance, dans les cycles saisonniers, entre la température et la nourriture. La méthode est également utile pour prédire l'impact possible des substances toxiques sur les taux de production de copépodes dans des conditions naturelles.

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SEVERAL methods are available for estimating biomass production rates of zooplankton. For example, for species which reproduce continuously, and do not display discrete cohorts, production can be calculated from a knowledge of the time spent in a given developmental stage, such as the egg, and the abundance of that stage in the field. Production can also be estimated from the difference between food assimilated and respiration (the carbon budget approach) (Edmondson and Winberg 1971; Tranter 1976). Such methods, although commonly used, have some disadvantages. In particular, production per unit biomass is not measured directly, but is estimated from a variety of parameters. Hence the effect of environmental perturbations which could influence production through any of several different mechanisms (e.g. reduced feeding, altered assimilation efficiency, increased mortality, growth inhibition, etc.) are often difficult to predict. Furthermore, the above procedures have usually led to an estimation of production for single species only. As an alternative, Tranter (1976) has suggested that total zooplankton production might be estimated by size fractionation using a battery of graded sieves. He proposed that incremental growth per organism in each size-group could be measured over short-time intervals.

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TABLE 1. The relative sizes of nauplii and copepodids collected between various sizes of nylon monofilament cloth filters.

Size fraction (mesh size in microns)	Relative mean sphere volume[a] (based on mesh sizes)	Relative copepod cylinder volume (based on length and width measurements of copepods)
64–102	1.0	1.0
102–153	3.7	2.8 nauplii 5.6 copepodids logarithmic mean = 4.0
153–202	10.3	11
202–275	24.8	27
275–363	59.8	69
363–505	149	170
505–656	362	290

[a]Used to estimate relative copepod biomass.

However, if the time interval is long enough to result in a considerable size increase in individuals, and if it can be demonstrated that artificial enclosure does not appreciably affect production (e.g. food is not used up within the experimental period) then manipulation of the incubation conditions can also provide estimates of the effect of environment perturbations (e.g. toxic substance addition) on zooplankton production. Below we describe a technique, based on size fractionation, which we have used to estimate growth and production rates of copepods in the surface waters of the Burlington Canal, and the influence of food conditions and temperature on these rates.

Materials and Methods

Copepod nauplii were collected from the Burlington Canal, which connects Hamilton Bay with Lake Ontario. The almost continuous current in the canal, with surface water usually coming from Hamilton Bay, provides a supply of surface water plankton and makes boat collections unnecessary. Nauplii were obtained by pouring up to 200 L of surface water, collected by bucket, through a pair of nested screens made of Nitex nylon monofilament cloth attached to the ends of sections of 3- and 4-inch (76- and 102-mm) diameter PVC pipe. Organisms collected in the upper screen of 102-μm pore size, which included all crustacean zooplankton except about 40% of the copepod nauplii, were discarded and the smaller nauplii, retained on the lower 64-μm screen, were used for experiments. Tests using finer mesh screens indicated that approximately 98% of all nauplii passing through 102-μm mesh netting are retained on 64-μm netting. The nauplii were transported to the laboratory in 4 L of canal water in a polypropylene jar and refiltered through a 102-μm screen to ensure elimination of larger plankton. After thorough mixing, a 250-mL subsample was filtered, fixed and stained using Lugol's solution, and counted under a microscope. An aliquot estimated to contain between 100 and 150 nauplii was then placed in an aluminum foil covered battery jar with sufficient canal water (previously filtered through a 44-μm screen to remove all crustacean zooplankton) to produce a final volume of 2 L. These were then incubated for 14 d at 15°C with a 12 h light: 12 h dark photoperiod. Deviations from the standard procedure were performed as required and are described in the appropriate section.

The temperature of the surface water in the canal was recorded at the time of collection, and a portion of the 44-μm filtered canal water was used for seston determinations. Seston was measured by filtering a known volume through prewashed, preashed, and preweighed, Whatman GF/C glass fiber filters, drying at 60°C, weighing, ashing at 500°C and reweighing.

After 14 d incubation, the copepods were filtered through a series of Nitex nylon mesh screens and counted. The relative biomass per individual of a given size-class, estimated as a volume (V) using the pore sizes of the mesh screens, is discussed in further detail below and summarized in Table 1. Total relative biomass was calculated by multiplying the number of organisms in each size-class by the estimated biomass per individual for that size-class (Table 1) and then summing the biomasses of all size-classes. The mean size per individual was then estimated by dividing the total biomass by the total number of organisms present. The growth rate (g) and mortality rate (m) were calculated using

$$(1) \quad V = V_o e^{gt}$$

$$(2) \quad N = N_o e^{-mt}$$

where V is the mean individual biomass, N is the number of organisms present, V_o and N_o are initial size and number, respectively, and t is time in days. The incubation period was not long enough to permit an increase in N through reproduction, although some females did bear eggs.

Results

Species identification was not attempted for nauplii or the smallest copepodid stages. Of all copepods large enough to be identified readily after 2-wk incubation, diaptomids always comprised less than 5%, the rest being Cyclopoids. *Cyclops vernalis* comprised about 80% of all identified copepods throughout the year except in the months of March, April, and May. In March it equalled approximately 60% and in April and May about 30%. The remainder of the copepods were *Cyclops bicuspidatus thomasi*. However, *C. vernalis* usually comprised the largest size-classes, appearing to grow faster than *C. b. thomasi*, and hence most of the unidentified copepods were probably *C. b. thomasi*.

The pore sizes of the screens used to filter the

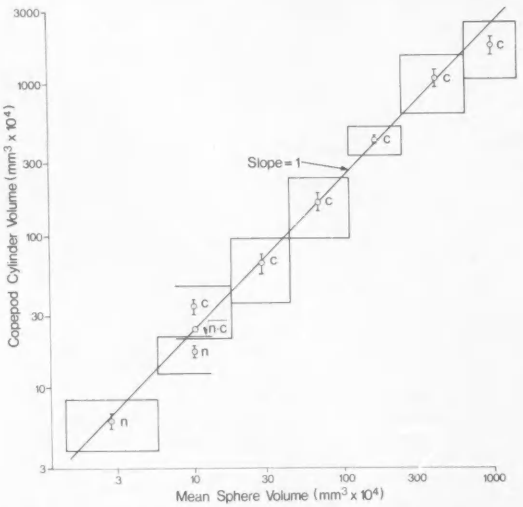

FIG. 1. Copepod cylinder volume (volume of a cylinder of length and diameter equal to copepod length and width) as a function of mean sphere volume (estimated volume of an average sphere retained in a given size-class). Vertical bars indicate 95% confidence limits. Width of boxes indicate sphere volume ranges, from spheres with diameters equivalent to the lower mesh size to those with diameters equivalent to the upper mesh size for each size-class. Height of boxes show mean ± one standard deviation unit for cylinder volume. Copepodids are indicated by *c* and nauplii by *n*.

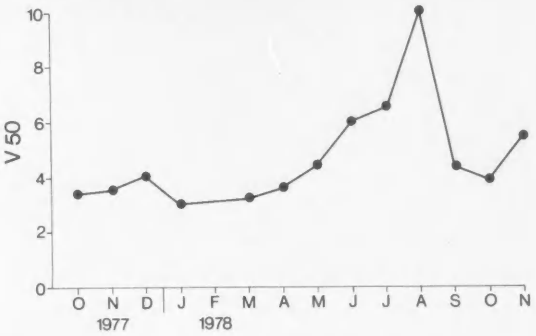

FIG. 2. Mean relative volume at which 50% of organisms were nauplii and 50% were copepodids (V50) for each month during the experimental period.

copepods are listed in Table 1. All copepods passed through the largest, 656-μm filter. In each size-class, 40 individuals were randomly chosen and measured for total length (excluding caudal rami for copepodids) and width. The volume of a cylinder of length equal to organism length, and diameter equal to organism width, was then calculated and plotted against the mean sphere volume for that size-class. Mean sphere volume is the logarithmic mean of the volumes of two spheres, one of diameter equal to the pore size of the filter on which organisms were retained, and the other of diameter equal to the pore size of the filter through which the organisms of that size-class have passed. This is shown in Fig. 1, along with the standard deviation and 95% confidence limits for copepod cylinder volume. For the 102–153-μm size-class, which at the time copepod volumes were estimated contained approximately 50% each of nauplii and copepodids, separate cylinder volumes are given for nauplii and copepodids, along with the logarithmic mean of these two volumes. A straight line of slope equal to 1 can easily be drawn through all the 95% confidence limits except for the largest size-class and the separate copepodid and naupliar sizes of the 102–153-μm group. The largest copepods are probably just barely large enough to be retained on the 505-μm filter, and hence are slightly smaller than expected for organisms retainable between 505 and 656 μm. The mean sphere volumes and copepod cylinder volumes, relative to the volumes of the smallest size-class, are listed in Table 1. As an estimate of the relative biomass per individual of a given size-class, the relative mean sphere volume was chosen rather than the relative copepod cylinder volume for two reasons. Firstly, mean sphere volumes are calculated from mesh sizes only, and hence can be recalculated rapidly if filter sizes are altered. For example, a size-group may be split into two by addition of an intermediate size filter. Secondly, the relative copepod cylinder volume might not remain identical if the sizes of the various stages in the copepod life cycle vary throughout the year. During the month of August, for example, the 102–153-μm size fraction contained mostly nauplii, and the 153–202-μm size-class, which earlier in the year contained only copepodids, now contained similar numbers of both nauplii and copepodids. The variation throughout the experimental period in the monthly mean estimated relative sphere volume (V50) at which 50% of organisms were nauplii and 50% were copepodids is shown in Fig. 2. It appears that maximum naupliar size may vary approximately threefold throughout the year. V50 was calculated by assuming a normal distribution for abundance of individuals of a given developmental stage as a function of logarithm of individual biomass. The probit of percent copepodids was plotted against the logarithm of relative sphere volume (i.e. 3.7 or 10.3) and the V50 estimated from the point on the plot opposite a copepodid concentration of 50%. For dates on which partial concentrations of copepodids were observed for only one size-class, V50 was calculated by extrapolating to the size equivalent to 50% copepodids using a line of slope equivalent to the mean of the slopes obtained for those dates when partial concentrations were obtained for both size-classes.

Although copepod biomass can be estimated from the pore sizes of filters used in sorting, this is not possible for all zooplankton. Cladocera, especially species

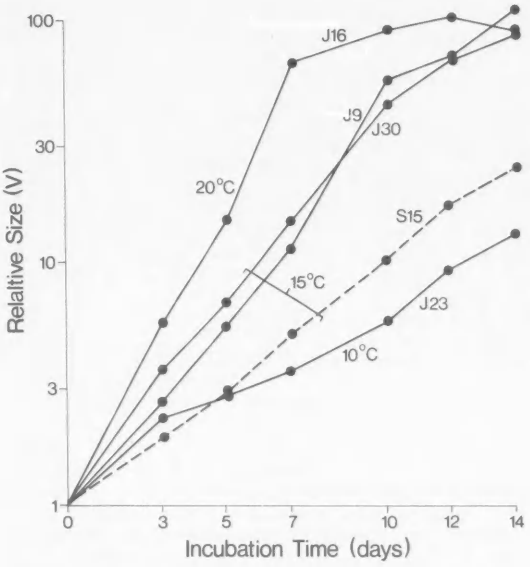

FIG. 3. Relative size of copepods as a function of incubation time at 10, 15, or 20°C on several dates during June (J) and on September 15 (S15).

such as *Bosmina longirostris* (which also tend to stick to the surface film), will be retained by filters of much larger pore size than expected on the basis of their body size.

The rate of increase of the mean size of copepods during the 2-wk incubation period at 15°C is shown in Fig. 3, along with similar studies conducted at 20 and 10°C. Although the growth is lower in September than in June, the rate of growth (g) appears to be relatively constant with time during each experiment until a maximum size, approximately 100 fold greater than the initial size, is approached. Hence the growth rate can be estimated fairly accurately from size measurements taken once, after 14 d at 15°C or 7 d at 20°C. The June data shown in Fig. 3 provide an estimate for the temperature dependence of g equal to a Q_{10} (rate at X°C divided by rate at (X-10)°C) of 3.3. The same Q_{10} was also obtained in October 1978, when several growth rate measurements were made at 20°C, as well as the usual 15°C.

Figure 4 shows the seasonal variation in the monthly mean growth and mortality rates, along with the temperature of the surface water in the canal and the seston (as ash free dry weight). Also shown is a temperature corrected growth rate $g(T)$, which is the estimated growth rate at a temperature equivalent to that measured in the canal using the observed monthly mean growth rate and a Q_{10} of 3.3. Although, as indicated by the seasonal variation in $g(T)$, the in situ growth rate must vary considerably throughout the year, the value of g as measured at 15°C is relatively constant,

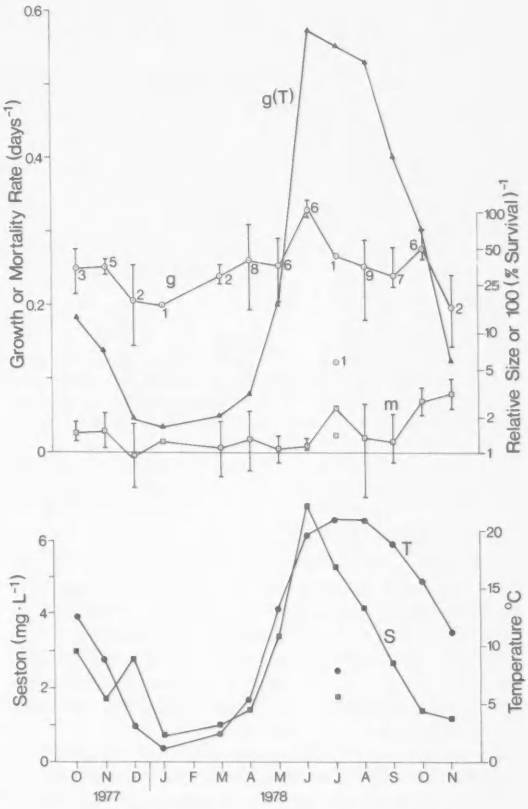

FIG. 4. Monthly mean growth rate (g), mortality rate (m), temperature of the surface water (T), and seston (S) as ash free dry weight, during the experimental period. Vertical bars indicate total range of values observed and numbers indicate number of experiments performed each month. The values of g, m, T, and S for July 27, when the surface water had an unusually low temperature of 8°C, are shown separately. Also included is $g(T)$, an estimate for in situ growth rates obtained by applying a Q_{10} of 3.3 to the growth rate (g) measured at 15°C.

usually lying between 0.2 and 0.3. (Although a growth rate of 0.3 is only 50% higher than one of 0.2, because of the 14-d duration of the experiment, this results in a final size increase of about 66 fold instead of 16 fold, producing a much higher final copepod biomass.) Exceptionally high growth rates were encountered in June, when g, measured on six occasions, ranged between 0.321 and 0.345. Growth rates this high were never encountered in any other month, and correspond with the peak in seston. Very low growth rates were observed once in December 1977 ($g = 0.157$) and once in November 1978 ($g = 0.144$). The lowest growth rate observed was 0.123, on July 27, 1978. On this date the surface water temperature was 8°C (down

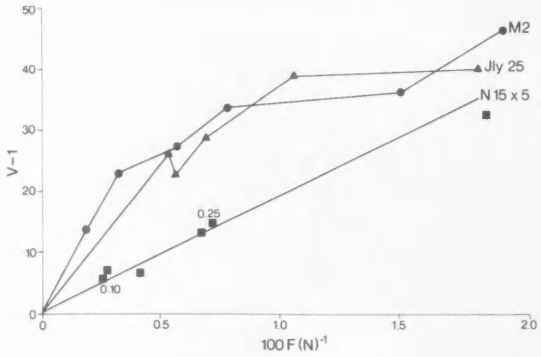

FIG. 5. Mean copepod biomass produced per individual ($V - 1$) as a function of food concentration divided by number of animals present (F/N) for May 2 (M2) when N was varied, July 25 (Jly25) when F was varied, and November 15 (N15) when F was 1.0 and N was varied except for two points, one with $F = 0.10$ and another with $F = 0.25$, as indicated in the figure. Biomass produced in November is multiplied by 5 to fit on the same scale.

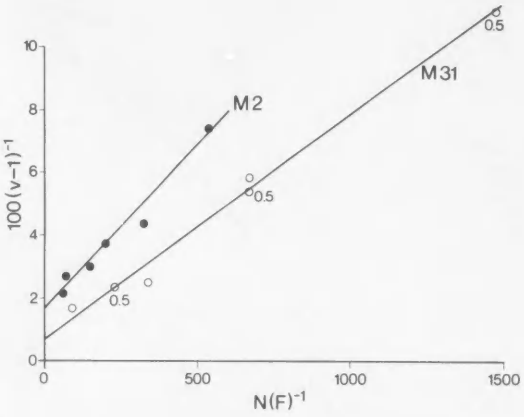

FIG. 6. Inverse of copepod biomass produced per individual $(V - 1)^{-1}$ as a function of the number of organisms present divided by the food concentration (N/F). On May 2 (M2) N was varied, and on May 31 (M31) three values of N were used for $F = 0.5$ (indicated in the figure) and $F = 1.0$. Lines were fitted by regression analysis.

from 21°C 2 d earlier), and the seston also was substantially lower, indicating that the normal current flow in the canal had probably been altered, making this observation not directly comparable with other dates. The monthly mean mortality rate m is also relatively constant throughout the year, total mortality averaging about 20% except in October and November of 1978 when it consistently exceeded 50%. The calculated mortality rate shows some variability from day to day and may be either positive or negative since the exact number of organisms initially present before incubation is not determined directly, but is estimated by counting a different subsample of presumably equal density.

To determine if the seasonal variation in growth rates was due to the food abundance in the canal water, experiments varying the relative food concentration (F) were conducted. This was done by filtering canal water through a Whatman GF/C glass fiber filter to remove the seston, and mixing this in various proportions with 44-μm filtered canal water. The highest food concentration ($F = 1$), consisted of pure 44-μm filtered canal water, as used in the standard procedure. Hence, the actual nutritional value of F is constant only for different treatments using water collected at the same time, since the quality and quantity of food organisms in canal water are not expected to remain constant from day to day. Experiments varying the number (N) of organisms present (the usual number being approximately 100 in 2 L of water per container) were also performed. Growth for both types of experiments can be described in terms of initial food concentration per individual per container (F/N). At very low F/N, all available food is probably consumed during the incubation period and therefore food concentration and growth rate cannot be expected to remain constant. Data are therefore analyzed in terms of total growth per individual (i.e. individual biomass after 14 d less initial biomass = V-1) instead of growth rate, and F represents initial food concentration only, not final or mean food concentration. Figure 5 shows V-1 as a function of F/N on several dates. On May 2, F/N was varied by varying N and holding F constant at 1. On July 25, only the food concentration, F, was varied. On November 15, 1978, N was varied and F held at 1 except for two points, one with $F = 0.10$ and one with $F = 0.25$. The November 15 experiment and another experiment varying both F and N on May 31 (see Fig. 6 and explanation below) indicate that the same relationship is observed between total growth and F/N, regardless of whether F or N is varied.

The total growth per individual was linearily related to food offered per individual (F/N) in November 1978 (Fig. 5). During the other months when F/N was varied, the relationship was hyperbolic, as for example, in May and July (Fig. 5). To express this data, the following equation was used

$$(3)\quad V - 1 = \frac{(V_m - 1)\,P_m\,(F/N)}{(V_m - 1) + P_m(F/N)}$$

$V - 1$ is the total biomass produced per individual, and V_m is the maximum size attainable by copepods within 14 d using canal water obtained on the experimental date under conditions of unlimited food per individual (F/N = infinity). V and V_m are in relative biomass units (1 unit = mean relative sphere volume for a nauplius in the smallest size fraction, 64–102 μm, Table 1). Growth rate under conditions of unlimited food,

TABLE 2. Maximum theoretical size attainable (V_m), growth rate (g_m), calculated from V_m, observed growth rate (g), maximum copepod production possible from 2 L of canal water (P_m), ash free dry weight of seston, and estimated minimum biomass production efficiency on various dates.

Date	V_m	g_m	g(% of g_m)	P_m	Seston mg·L^{-1}	Minimum efficiency
May 2	61(43–105)[a]	0.294	0.275 (94)	9,690 (7,760–12,890)[a]	2.9	7.5%
May 31	142(71–∞)	0.345	0.292 (82)	14,000 (12,300-16,200)	6.2	5.1%
July 25	60(41–116)	0.292	0.269 (92)	7,810 (5,240–15,400)	5.3	3.3%
July 27	4.1(2.7–21)	0.101	0.123 (122)	1,930 (1,210–4,790)	1.8	2.4%
Aug. 22	32(22–54)	0.248	0.275 (111)	43,600 (24,700–184,000)	5.2	18.9%
Sept. 12	24(11–∞)	0.227	0.238 (105)	12,400 (8,680–22,100)	0.9 (2.7)[b]	31.2% (10.4%)
Nov. 15	—	—	0.144	374	0.8	0.9%
Nov. 16	—	—	0.245	1,200	1.6	1.7%

[a]95% confidence limits.
[b]Mean seston for month of September.

and hence independent of food concentration, would be calculated from V_m. Since growth rates calculated from V_m are theoretically independent of food concentration, seasonal variations in these rates (and V_m) must be due to qualitative differences in food, or other factors.

As F/N approaches 0, equation 3 simplifies to

$$(4) \quad V - 1 = P_m(F/N)$$

If F is equal to 1, equation 4 leads to

$$(5) \quad P_m = N(V - 1)$$

Hence, P_m is the biomass produced per individual times the number of individuals present, which equals the total copepod biomass production possible (in relative biomass units) from 2 L of canal water if N is high enough to permit utilization of all available food. P_m, therefore, is a measure of food concentration, unless food quality affects copepod biomass production efficiency, in which case P_m is a function of both food quality and quantity.

To calculate P_m and V_m equation 3 can be inverted. Hence a plot of $(V - 1)^{-1}$ versus N/F should give a straight line of slope $P_m{}^{-1}$ and Y intercept $(V_m - 1)^{-1}$. Examples of such a plot are shown in Fig. 6, for May 2, when N was varied, and for May 31, when three values of N were used for each of $F = 1$ and $F = 0.5$. Similar plots were used for experiments in which F was varied on July 25 and 27, August 22, September 12, and November 16, 1978. For each date, a regression analysis was done to obtain estimates of P_m and V_m. The results are listed in Table 2. By adding or subtracting the corresponding 95% confidence intervals obtained from the regression analyses to the Y intercept and slope before taking the inverse, the confidence intervals included in Table 2 were obtained. On two occasions, subtracting the 95% confidence interval from the Y intercept gave a negative number, resulting in no upper confidence limit for V_m. In November, the relationship between $V - 1$ and F/N appeared to be linear instead of hyperbolic, and hence V_m could not be calculated and P_m was estimated by dividing the mean for all $V - 1$ by the mean for F/N.

V_m was highest on May 31 (although only statistically significantly higher than on August 22). This date is close to the month of June when the highest growth rates were observed (Fig. 4). The low V_m for July 27 coincides with a surface water temperature of 8°C and reduced seston resulting from altered current flow in the canal. Growth rates (g_m) calculated from V_m are compared with the observed growth rates in the control (g) in Table 2. Except in the month of November, g was close to g_m, indicating that food is not usually limiting if approximately 100 animals are raised in 2 L of canal water under our experimental conditions. This is not surprising since growth rate appeared to be constant with time during the experimental period, at least until maximum size was obtained (Fig. 3). Hence the high growth rates observed in June are not simply a function of higher food concentrations, but indicate a difference in food quality or some other parameter. On the other hand, the growth on November 15 and 16, 1978, appeared to be food limited, and an accurate value for V_m could not be calculated (see Fig. 5).

The low value for P_m observed July 27, suggested that the concentration (or quality) of acceptable food items in the 8°C water collected that day was very low. Similarily, P_m was also very low in November, which is not surprising due to lower temperatures and reduced daylight at this time of year. For the other months, P_m values were not significantly different, with the exception of August. It is interesting to note that the highest P_m, which suggests the highest food concentrations, did not occur in June, when seston and growth rates were highest, but occurred in August, when the maximum size obtained by nauplii (V50, Fig. 2) was greatest. Seston is obviously not directly proportional to the concentration of the preferred food of these copepods.

A rough estimate of ecological efficiency can be ob-

TABLE 3. Initial size (V_o), final size (V), and growth rate (g) for copepods raised on canal water filtered through 44- or 20-μm screens, or filtered through glass fiber filters with addition of particules retained between 20- and 44-μm screens.

Date	Food size μm	Seston[a]	Duration of Experiment	V_o	V	g (d^{-1})	Estimated g for second week only
Aug. 2	0–44	4.1	1 week	1.0	10.1	0.330	—
	0–20	3.1	1 week	1.0	10.7	0.339	—
	20–44	1.0	1 week	1.0	3.58	0.182	—
Aug. 2	0–44	4.1	2 weeks	1.0	49.2	0.278	0.226
	0–20	3.1	2 weeks	1.0	25.9	0.232	0.126
	20–44	1.0	2 weeks	1.0	10.6	0.169	0.155
Sept. 13	0–44	3.2	1 week	1.0	3.76	0.189	—
	0–20	1.5	1 week	1.0	4.38	0.211	—
	20–44	1.7	1 week	1.0	2.07	0.104	—
Sept. 13	0–44	3.2	1 week	10.3	70.4	0.275	—
	0–20	1.5	1 week	10.3	31.6	0.160	—
	20–44	1.7	1 week	10.3	42.8	0.203	—

[a]$mg \cdot L^{-1}$ ash free dry weight.

tained by dividing P_m by the food concentration. To do this, P_m was multiplied by the ash free dry weight per relative biomass unit and divided by 2 (to convert from relative units per 2 L to $mg \cdot L^{-1}$), and then divided by the ash free dry weight of the seston. The ash free dry weight per relative biomass unit was obtained by weighing 50 *C. vernalis* from each of the 275–363 and 363–505 μm size-groups, after drying and ashing, on a Cahn electrobalance and dividing by the relative biomass per individual (59.8 and 149, respectively). A mean value of 4.5×10^{-5} mg (ash free) per biomass unit was obtained (ash weight = 6% of dry weight). Results (Table 2) indicate that efficiency of conversion of seston into copepods was highest in August and September, even though g was higher on May 31 (this observation holds even if the high September efficiency is suspected to be the result of an erroneously low seston estimate for that date, and the monthly mean seston is used instead). Hence, food quality appears to have been highest in late summer, but deteriorated substantially by November. Since the proportion of the seston which actually constitutes a usable food source is not known, these efficiency estimates should be considered as minimum estimates of true efficiencies only. Nevertheless, these efficiencies are similar to those reported for other zooplankton (e.g. Tranter 1976; Parsons et al. 1977).

As noted above, F in equations 3 and 4 represents initial food concentration only, and therefore growth or mortality of food organisms during the incubation period could influence the accuracy of ecological efficiency estimates made from P_m. Our experimental containers had aluminum foil covers preventing direct illumination and hence minimizing any algal growth that might have occurred. For more accurate estimates of ecological efficiencies, the species used as a food source should be identified and conditions controlled so as to keep its concentration constant in controls without copepods. Since V_m is independent of F, variations in food concentration would not affect its calculation.

The growth rate is affected not only by the food concentration, but also by its size, and optimum food size is a function of the size of the copepods. This is shown in a food size fractionation experiment summarized in Table 3. Normally, canal water was filtered through 44-μm screens to remove crustacean zooplankton before being used as a food source. Further filtration through a 20-μm screen does not impair the growth of copepods during their first week in development at 15°C. Furthermore, nauplii do poorly on food particles retainable on a 20-μm filter. On the other hand, during their second week of growth, or if larger individuals are used to initiate the experiment, growth is greater on the 20–44-μm fraction than on the water filtered through 20 μm. Some benefit is still obtained from particles less than 20 μm in size, however, since growth is best if both fractions are present.

One other factor which was observed to affect growth was the ash weight of the seston. This value became high occasionally in spring and fall, immediately after stormy weather. Highest ash weights were observed in December, 1977. On December 5, with an ash weight of 50.6 $mg \cdot L^{-1}$ (ash free dry weight of 2.5 $mg \cdot L^{-1}$), g was 0.157. Two days later the ash weight had dropped to 19.0 $mg \cdot L^{-1}$ (ash free dry weight = 3.0 $mg \cdot L^{-1}$) and g rose to 0.254. On all other dates, ash weight was below 12 $mg \cdot L^{-1}$, and did not noticeably affect growth rates.

Discussion

This paper describes a rapid method for measuring copepod production rates by sorting organisms to size

using nylon monofilament screen filters. Size increase is determined as a function of time and biomass production is calculated directly. The increase in size was logarithmic (Fig. 3), indicating a constant growth rate until a maximum size was reached. Other authors (e.g. Miller et al. 1977; McLaren 1978) have implied the existence of logarithmic growth by demonstrating isochronal development (equal time spent in each developmental stage) and assuming a constant relative increase in size from one stage to the next. However, determining size directly by sorting organisms through screens and counting is much more rapid than determining stage of development and biomass per stage. The present technique, for example, has permitted the estimation of the mean biomass and growth rates for approximately 600 copepods (1 control plus 5 treatments with 100 animals each) on a daily basis. Because of their small size, direct weighing of all individuals would be difficult, especially in experimental treatments resulting in low growth, where at the end of the incubation period most individuals may still be nauplii.

Since copepods were collected from the field, the nauplii used to initiate experiments represent a natural assemblage of species (mainly *Cyclops vernalis* and *C. bicuspidatus thomasi* but including a few diaptomids), and hence growth rates provide an overall estimate of copepod production, rather than a measure of production for any one species. All individuals were of similar size initially and predation of one species on another, or cannibalism would therefore be minimized.

Results indicate that for copepods from the Burlington Canal the daily growth rate at 15°C may range from 0.123 (July 27) to 0.345 (June 7) but usually lies between 0.2 and 0.3 ($Q_{10} = 3.3$). The mean growth rate for all dates was $g = 0.258$. The increase in size during the incubation period is fairly large (e.g. a 37 fold increase if $g = 0.258$), resulting in fairly accurate estimates of g. Survival is usually about 80%, although values as low as 24 and over 100% (due to inaccuracy in the estimate for N) have been recorded. Estimates of mortality rate (m) are not as accurate as those for g. The average for m, excluding October and November, 1978, when unusually high mortality occurred, was 0.017. The average for all m was 0.025.

The values for g and m can be combined to give the cohort biomass growth rate ($k = g - m$), which averaged 0.233. This is equal to the rate of increase in biomass of the population in the absence of predation. The rate of biomass production per unit biomass, which includes the increase in biomass plus the biomass produced by dead organisms up to the time of their death, is given by g, if growth is exponential (e.g. equation 1, Fig. 3), regardless of the nature of the mortality function (Allen 1971). Hence, the rate of copepod biomass production in the Burlington Canal could be estimated from gB_c where g is the growth rate corrected for temperature (Fig. 4) and B_c is the biomass in the canal. However, the portion of the biomass production not lost to natural mortality, and hence available to higher trophic levels, is given by kB_c. These estimates apply accurately only to the growth phase of the life cycle of copepods. Appropriate corrections have to be made for large nongrowing members of the population if their contribution to production (i.e. through reproduction) differs from that of smaller, actively growing individuals.

Although copepods were incubated in the laboratory, the source of experimental animals was a field population, the water was obtained from the field, and the food used consisted of whatever was available in this water. Hence growth rates, after extrapolation to field temperatures, should be similar to those observed in the field. Estimates of zooplankton production in the field, for organisms which do not show discrete cohorts, have frequently been made by determining development time for a selected stage (usually the egg) and measuring relative abundance of that stage in the field population (e.g. Edmondson and Winberg 1971). The present technique, however, has the advantage that the incubation time covers a major period in the life cycle of copepods (from early nauplii to late copepodid stages), thereby permitting experimental manipulation of environmental conditions during growth. Hence, the significance of in situ food concentrations or the effect of temperature or toxic substances on production under natural conditions can be estimated.

By manipulation of food concentration, it was possible to obtain data which suggests that food concentration was not limiting copepod growth rates from May to September (i.e. $g = g_m$, Table 2). Furthermore, the food concentration in canal water (as estimated from P_m) appeared to be highest in August, and hence was not directly proportional to seston. Food manipulation also made it possible to obtain rough estimates of ecological efficiencies, in terms of weight of copepods producible from the seston available in canal water (Table 2). Also, by fractionating the food particles using a 20-μm filter it was shown (Table 3) that, for species present in the Burlington Canal, copepod nauplii grow better on small food particles and later stages grow better on larger food. Although changes in the feeding habits of copepods with size are well recognized (e.g. Dodson 1975), the data in Table 3 indicate not just feeding preferences, but the ability of various sizes of copepods to grow on various sizes of food.

The results of the experiments on manipulation of food concentration are perhaps most interesting if compared with the available information on temperature effects. Using the present technique, g was measured at a constant temperature (15°C) and hence any deviations from the mean might be due to variations in food. Apparently, food was limiting in November (at least in 1978, Table 2) and presumably also in December and January (Fig. 4). However, excepting June, with high g values (though not believed to be due to unusually high food concentrations, Table 2), g was remarkably uniform during much of the year. The esti-

mates of in situ growth rates ($g(T)$) suggest that temperature exerts a far greater influence on growth than does food concentration (Fig. 4). These results are similar to the observations of McLaren (1978), who noted that growth rate predictions made from temperature data alone, assuming no effect of food concentration, matched reasonably well with observed growth rates in the field. This does not imply that food concentrations are unimportant in the ecology of copepods. The high temperature sensitivity of these animals may be a feature which permits them to anticipate food levels, due to the similarity in the seasonal cycles of temperature and food abundance (note similarity in temperature and seston cycles, Fig. 4). Adaptation to altered food concentrations may therefore be indirect, resulting in the high temperature sensitivity. Hence, McLaren's (1978) suggestion that more study should be made of "intrinsic" adaptations that determine copepod performance in nature, rather than simply relying on studies of feeding physiology and trophic ecology, seems appropriate.

Food and temperature may influence not only growth rate, but also the final size reached by copepods. In general, individuals grow largest when temperature is lowest or the food concentration is highest (e.g. Deevey 1960). In some studies however, a positive correlation has been observed between temperature and copepod size in the field (e.g. Evans and Diaz 1978). Such a correlation might be due indirectly to a positive correlation between temperature and food. Unfortunately, when both food and temperature vary simultaneously, the effect of either variable may be difficult to separate from the effect of the other. Consequently, the apparent food effect suggested by one author may be disputed by another (e.g. McLaren 1963). In the present study, however, since temperature was held constant, the effects of seasonal factors other than temperature on copepod size can be clearly demonstrated. The largest size obtained by nauplii was observed in August (Fig. 2) corresponding to a maximum in P_m (Table 2). This suggests that factors other than temperature (possibly food quantity or quality) may considerably influence copepod size, even though their influence on growth rates is small (Fig. 4). It is also possible that some of the size increase in nauplii in August was due to a shift in species composition, although the species composition of copepodids appeared to be relatively consistent throughout most of the year. The present technique has at least made it possible to separate the effect of temperature from the other factors influencing size.

Another application of the procedure described here is the estimation of the effects of toxic substances on copepod production. Since a considerable amount of growth occurs during the incubation period (e.g. mean size increase = 37 fold), the effect of toxicants on biomass production, either through reduced growth or increased mortality, can be determined. Although the experimental duration is only 2 wk at 15°C (1 wk is sufficient at 20°C), because of the rapid growth of these organisms, such a test constitutes a measure of sublethal toxicity. Exposures of similar duration with fish or other large organisms can usually only provide data on lethal toxicity. Furthermore, since experiments are conducted using natural populations of copepods, natural water, and natural food, results should be directly applicable to field conditions.

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Establishment of Sockeye (*Oncorhynchus nerka*) and Chinook (*O. tshawytscha*) Salmon Runs at Frazer Lake, Kodiak Island, Alaska

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BLACKETT, R. F. 1979. Establishment of sockeye (*Oncorhynchus nerka*) and chinook (*O. tshawytscha*) salmon runs at Frazer Lake, Kodiak Island, Alaska. J. Fish. Res. Board Can. 36: 1265–1277.

Runs of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) were established at Frazer Lake, Kodiak Island, Alaska by adult spawner transplants, fry plants, and eyed-egg plants. Falls in the lake outlet formed a barrier to natural ascent of anadromous fish until construction of a fishpass in 1962. Accounts of successful introduction and development of viable and self-sustaining runs of salmon where none previously existed and the lake was inaccessible are scarce in the history of salmon fisheries on the Pacific Coast. The first sockeye returning to Frazer Lake in 1956 were produced from egg plants in 1951. Annual sockeye returns have progressively increased over a 28-yr period reaching record passage of 141 981 in 1978. Sockeye spawning has extended into new areas as returns increased. Spawning area capacity is projected to be sufficient for 365 000 sockeye while rearing area is estimated to be sufficient to support fry production from 400 000 sockeye. Sockeye returns per spawner have averaged 3.2 for six parent years (1966–71) in which returns are complete. A chinook run was created from plants of 160 000 fry over a 4-yr period beginning in 1966. Chinook have returned to spawn in specific sites of fry release above the falls and in the lower river.

Key words: salmon introduction, enhancement technique, sockeye, chinook, Frazer Lake, salmon establishment

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Grâce à des peuplements de reproducteurs adultes, ensemencements d'alevins et d'oeufs oculés, des montaisons de saumons nerka (*Oncorhynchus nerka*) et chinook (*O. tshawytscha*) se sont établies dans le lac Frazer, île Kodiak, Alaska. Jusqu'à ce que l'on ait construit une passe migratoire en 1962, des chutes dans l'émissaire du lac constituaient une barrière à la remontée naturelle des poissons anadromes. Il y a très peu, dans l'histoire des pêcheries de saumon de la côte du Pacifique, de rapports d'introductions réussies et d'établissements de montaisons de saumons viables et autonomes là où il n'en existait pas auparavant et où le lac était inaccessible. Les premiers saumons nerka à retourner au lac Frazer en 1956 provenaient d'ensemencements d'oeufs en 1951. Les remontées annuelles de saumons nerka ont augmenté progressivement sur une période de 28 ans, atteignant un pic de 141 981 poissons en 1978. Avec l'augmentation des retours, les saumons nerka ont élargi leurs aires de fraie. On prévoit que la superficie des frayères pourra accomoder 365 000 saumons nerka, alors que les aires d'alevinage suffiraient à supporter la production d'alevins de 400 000 saumons nerka. Les retours de saumons nerka par reproducteur ont été en moyenne de 3,2 pour six années-parents (1966–71) dont on a des données complètes. Une montaison de saumons chinook s'est établie à partir d'ensemencements de 160 000 alevins sur une période de 4 ans à commencer en 1966. Les saumons chinook sont revenus frayer à des endroits spécifiques de mise en liberté d'alevins en amont des chutes et dans le bas de la rivière.

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SOCKEYE salmon (*Oncorhynchus nerka*) were first introduced into Frazer Lake on Kodiak Island in 1951 to create a run into a lake system that was blocked to anadromous fish by falls in the outlet stream. An extensive program of sockeye egg and fry plants, adult transplants, fishpass construction and operation at the falls, and evaluation of the run has been conducted by the Alaska Department of Fish and Game (Department of Fisheries prior to 1957) for 28 yr. This enhancement effort has been highly successful in establishing a new sockeye stock of substantial magnitude (141 981 escapement in 1978) and benefit to the commercial salmon fishery in the Kodiak area.

This project has not been documented in a single publication covering the entire span of development. Also, the development of a chinook salmon (*O. tshawytscha*) run from fry plants at Frazer Lake has

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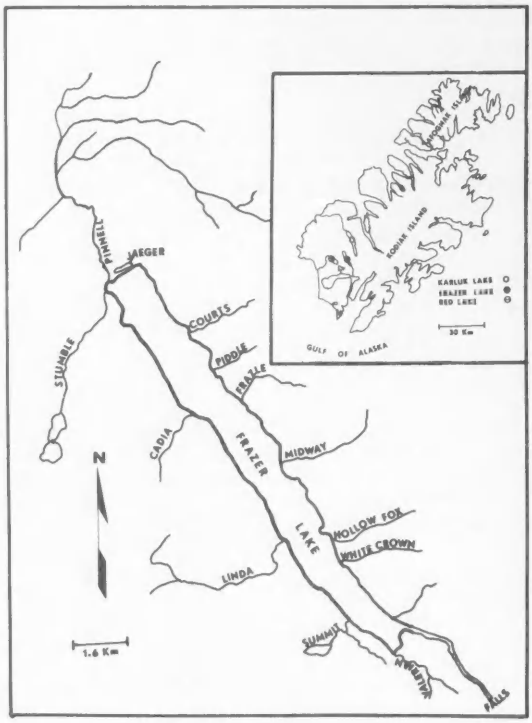

FIG. 1. Frazer Lake and location of Karluk and Red Lake donor sockeye stocks on Kodiak Island, Alaska.

not been reported. Progress reports by Meehan et al. (1965), Eaton and Meehan (1966a, 1966b), Eaton (1967, 1968), Gwartney (1969), Russell (1972), Blackett et al. (1969, 1970), and Blackett (1973) have periodically described lake characteristics, smolt migrations, and adult sockeye returns. The purpose of this paper is to document the establishment of sockeye and chinook salmon at Frazer Lake.

HISTORICAL BACKGROUND

Frazer Lake, located on the southwestern end of Kodiak Island at 154°10′W and 57°15′N (Fig. 1), is 12.9 km long and 1.6 km wide with a surface area of 6.7 km^2 and a volume of 557.06×10^6 m^3. The second largest lake on Kodiak Island, it is situated on the Kodiak National Wildlife Refuge 108 m above sea level, midway (6.4 km) between Karluk and Red lakes which are both famous for historic production of sockeye salmon (Gilbert and Rich 1927; Hennick and Bevan 1970) and still are major producers of sockeye. These lakes provided donor stock for introduction into Frazer Lake. Frazer falls, which blocks passage of anadromous fish, is 1.6 km downstream from the lake and 9.6 km from Olga Bay.

Cursory studies of Frazer Lake conducted in the early 1950s indicated the lake system was favorable for sockeye spawning and rearing (C. E. Stockley, Alaska Dep. Fish., unpublished data 1953). The impassable 10-m high falls was thought to be the only reason sockeye did not occur naturally. Only resident populations of rainbow trout (*Salmo gairdneri*), Dolly Varden char (*Salvelinus malma*), three-spine stickleback (*Gasterosteus aculeatus*), and coastrange sculpin (*Cottus aleuticus*) were known to exist in the lake. Pink (*O. gorbuscha*) and chum (*O. keta*) salmon were present in the river below the falls.

In August of 1951, 200 000 sockeye eggs were taken from Karluk Lake shore spawners and planted as green eggs in Stumble Creek, a tributary of Frazer Lake. This first egg plant had minimal success due to high water causing the eggs to drift out of the gravel during planting. Sockeye fry, however, were captured in a seine off the creek mouth in June of the following year. Between 1951 and 1956, 2.97 million sockeye eggs taken from shore spawners at Karluk Lake and tributary spawners at Red Lake were planted at Frazer Lake.

Evaluation of early planting efforts began when the first adult sockeye returned to Frazer falls in 1956. Traps and a wire fence were installed in the river below the falls to count sockeye returns and smolt migrating downstream to Olga Bay. The weir was ineffective as only five adult sockeye and one smolt were captured in the traps while an estimated 500 adults were observed jumping at the falls (Alaska Department of Fisheries 1957). In spite of weir problems, the first return of approximately 500 sockeye from an initial egg plant of 200 000 was an obvious success.

Materials and Methods

DONOR SOURCES AND PLANTS

The primary donor source for sockeye introductions into Frazer Lake has been Red Lake stock. Egg takes and adult transplants were from the June–July portion of the run which typically spawned in the tributary streams. Karluk sockeye provided eggs for the initial 1951–54 plants and in 1969, eggs were taken at Becharof Lake on the Alaska Peninsula from sockeye that would have spawned in August and September in the outlet stream of a tributary lake. In 1955 and 1956, sockeye eggs were incubated in troughs at an inoperative cannery at Olga Bay until they were eyed. After 1960, eggs were transported by air to the Kitoi Bay Hatchery on Afognak Island for incubation to either eyed eggs or fry.

Eggs for chinook fry introductions into Frazer Lake were taken from Karluk River spawners each year from 1965 through 1968 and incubated at the Kitoi Hatchery.

Early egg planting technique was to blast the streambed of the recipient creek with 1- or 2-stick charges of 40% dynamite prior to each egg plant to loosen gravel for shoveling and planting (Stockley 1954). In 1951, a hole about 1-m diameter and 30–45 cm deep was dug with a shovel and the eggs buried. To avoid the problem of eggs drifting downstream, an egg planting tube of drainpipe was designed in 1952 that could be inserted into the streambed and the eggs poured down the tube into the gravel. Stockley (1954) describes this method of planting and noted that a crew of three men could plant a million sockeye eggs in 12 h. An estimated 20 000–23 000 eggs were planted in

each hand dug "redd." Eggs were treated with malachite green before the tube was withdrawn.

In 1954, the tube was replaced by a cylinder approximately 50 cm in diameter and 90 cm high. The method described in the Alaska Department of Fisheries Annual Report (1956) was to dig trenches parallel to the current in suitable streambed sites. Two cylinders were placed at the upstream end of the trench, one downstream from the other. A few large rocks, about 15 cm in diameter, were placed in the upstream cylinder and from 1000 to 8000 eggs poured in. When the eggs had settled into the interspaces of the rocks, gravel from the streambed was shoveled into the cylinder until it was slightly higher than the surrounding streambed. The first cylinder was then removed and placed in the trench downstream from the second cylinder and the process repeated until the trench was filled with eggs. The cylinder method was considered superior to the tube in egg distribution and speed of planting.

The cylinder method was used at Frazer Lake throughout the remaining egg plants, but with some variation in technique. Instead of trenches, circular pits were dug in the streambed during low flow periods in the summer and one-third sections of 208-L drums sunk into the pit to retain it for fall egg planting. During the egg plant, debris was flushed from the pit and the cylinder slipped into the drum section. Eggs and gravel were placed in layers within the cylinder. After egg planting, gravel was shoveled between the outside of the cylinder and drum to keep the eggs from drifting out during removal of the cylinder and drum section. The process was then repeated for each predug pit. This technique increased the speed and capability for production planting of 2.0–3.0 million eggs per day.

From 1967 to 1969, eyed eggs were held in the hatchery until an advanced stage of development, 2–3-wk before softening of the outer chorion and hatching. Planting at this stage shortened the period of egg concentration before alevin dispersal in the gravel and increased likelihood of fry survival from high density plants of 20 000–25 000 eggs.

Sockeye fry incubated and reared for 1 mo at Kitoi Hatchery were planted between May 15 and June 15 at approximately 6600 to 7300/kg. Fry were taken off feed 24 h before planting. About 11 000 fry were placed in a 68-L polypropylene container half-full of water. Each container was filled with compressed oxygen until firm.

An amphibious goose aircraft transported up to 18 containers per trip on the 45-min flight to Frazer Lake. The containers were occasionally shaken during the flight to oxygenate the water. Upon landing at the head of Frazer Lake, all of the containers were floated in the lake and the fry released. This allowed the aircraft to depart immediately for another trip to Kitoi Hatchery and also provided time for water temperature in the containers to adjust to lake temperature.

All of the sockeye fry in 1971 were flown by helicopter 8 km up Pinnel Creek, the main inlet stream. The purpose of this tributary release was to imprint the fry and develop a return of adults to previously unutilized spawning area.

Chinook fry were transported from Kitoi Hatchery in the same manner as the sockeye, but released in the lake outlet and below the falls in the Frazer River.

Transplants of adult sockeye from Red Lake to Frazer Lake were begun in 1958. Eight to ten adult sockeye were transported in a water filled drum in a Piper Supercub Aircraft. After landing at Frazer Lake, 8 min later, the fish were removed by hand and released in Midway Creek.

In 1963, an aluminum tank capable of holding 76 L of water, was mounted on each float of a Supercub. Water was pumped into the float tanks and fish dipnetted from live boxes into aluminum chutes leading into the tanks. Loading of both tanks could be accomplished in less than 12 min. A maximum of 30 sockeye (15 per tank) could be transported from Red Lake to Frazer Lake in 20–25 min per round trip. Upon landing at Frazer Lake the tanks were rotated and the fish released by a pilot operated control. This method greatly increased the efficiency of aerial transplants as the entire release operation was performed by the pilot without stopping the aircraft. A weir across the Frazer Lake outlet prevented transplanted sockeye from leaving the lake.

FIG. 2. Frazer River falls at the lake outlet showing fishpass facilities.

FISHPASS OPERATION

Sockeye returning to Frazer Lake from 1956 through 1962 were backpacked over the falls in water-filled metal containers strapped to a pack board. A steeppass fishway of Denil design described by Ziemer (1962) was constructed at the falls in 1962. The 64 m long structure (Fig. 2) consists of parallel runs of steeppasses in four steps with three concrete resting pools, a vertical slot entrance, diversion weir, and exit tank at the top of the falls.

The fishpass is operated for the duration of the sockeye, chinook, pink, and chum salmon runs which occur between June 1 and August 30. Fish passage is monitored at the top exit tank where all salmon are counted by species before release upstream. The top tank has a capacity for

about 2500 salmon, requiring counting and release at least hourly during peak passage periods.

Evaluation of Salmon Introductions

Evaluation of sockeye and chinook introductions and development at Frazer Lake, has consisted of determining (1) magnitude and composition of the adult salmon return to the fishpass, (2) spawning area distribution and utilization, and (3) smolt outmigration timing, composition, and magnitude.

Salmon returns counted annually since 1956 at the Frazer falls and at the fishpass provide the ultimate evaluation of the success of sockeye and chinook introductions. Sockeye and chinook adults were sampled at the fishpass for age, length, weight, and sex data. Sampling schemes have varied over the years, but since 1975, 100 adult sockeye were sampled each week (20 each day for 5 d) and all chinook captured at the counting gate were sampled. Fish were anesthetized in a MS 222 solution, measured from mid-eye to tail-fork to the nearest millimetre and weighed to the nearest 0.10 kg. Sex was determined from external characteristics. Scales were taken from each fish for determination of age. All fish were released upstream upon recovery.

A smolt weir was successfully operated from 1965 to 1971 to determine smolt migration timing and magnitude. Smolt samples were taken at the weir for size and age composition. The smolt weir became impractical by 1971 due to the increasingly greater number of smolts leaving the lake each spring, combined with high water and mortality problems. Smolt were sampled from 1971 to 1974 by using index nets. From 1975 to 1978, smolts have been collected by seining every other day below the falls. The number of smolt caught per seine haul provided a relative index of migration timing. The only assessment of the number of smolt leaving the system since 1970 has been cursory observations of concentrations below the falls.

Samples of 40 smolt were taken from the seine for age and size data. Smolts were dip netted from the seine bag into a container of MS 222 solution. Anesthetized smolts were measured from snout to tail-fork to the nearest 0.1 mm, and weighed to the nearest 0.1 g. Scales were taken for age analysis. All fish were placed in a recovery container before release downstream. Otoliths were taken from dead smolts to verify age determinations from scales.

Annual spawning ground surveys have been conducted during the sockeye spawning period at Frazer Lake since 1964. Two observers independently counted the number of live and dead salmon per 0.1-mi (0.16-km) section of creek and recorded an average count for each section of the entire spawning area. Each tributary was surveyed at least three times throughout the season. Lake shore surveys were conducted by boat on calm days and the number of sockeye recorded on a shoreline map. The number of paired spawners, intensity of spawning activity, and number of unpaired sockeye were noted. During the peak of the spawning period, an aerial survey was conducted of the entire lake system to estimate the number of live and dead sockeye on each spawning area.

Lake Studies

Echo sounding was conducted in 1970 to determine juvenile sockeye distribution in the lake. A recording fathometer was operated at a frequency of 190–200 kHz with a transducer beam angle of 22° (Russell 1972). Initial sensitivity was tested with a 150 mm sockeye smolt attached to a light nylon line weighted with a lead sinker. The smolt and lead weight were both detectable at a depth of 30 m.

The diurnal movement of young sockeye was charted by running a series of transects across the lake in the same location during evening, night, and early morning in mid-May and early August. Chart recordings were compared to rearing behavior in the lake during spring and summer.

Sockeye spawning area was surveyed in 1975 to determine optimum escapement and distribution at Frazer Lake. For the tributaries, two or more observers walked each stream and measured width at 0.1-mi (0.16-km) intervals to determine stream area. A qualitative rating expressed as a percentage of suitable area for spawning was given each section. A uniform gravel composition of 1.5–3.5 cm rock with optimum water depth and flow was set as a standard for a maximum (100%) rating. Presence of boulders, sand areas, poor flow, etc., would result in a lower rating; i.e. 80% of stream area of a quality suitable for spawning and egg survival. The final rating was usually a compromise of individual observer ratings. Lake shore spawning area was surveyed the same way except from a skiff. Shore spawning area and quality were plotted by section on a map. Optimum sockeye escapement was calculated at a density of one female per 2.0 m^2 of spawning area and an equal male to female sex ratio.

Lake rearing capacity for young sockeye was projected from depth profile mapping and computation of total lake volume, depth of sockeye rearing (echo-sounding results), and optimum sockeye fry density information from experimental plants in rehabilitated lakes at Kitoi Bay, Afognak Island (Meehan 1966).

Zooplankton has been sampled annually at Frazer Lake since 1965 to monitor changes in density and composition. Vertical hauls of a 0.5-m diameter, 153-μm plankton net were made once a week to depths ranging from 15 to 55 m at each of four stations from May through August. Sampling stations, located in a mid-line the length of the lake, were marked by buoys to standardize locations throughout the sampling period. Each sample was washed into a bottle containing formalin preservative and examined within 3-wk using a Sedgewick-Rafter counting cell, 0.05-mL test cell volumes ($n = 5$) and 125-mL sample volumes. Zooplankton was identified to genus and density expressed in number per cubic metre.

Water temperature (surface and depth profile) and water chemistry (dissolved oxygen, alkalinity, total hardness, free CO_2, and pH) were recorded at one of the plankton sampling stations each week. Water chemistry measurements were taken with a Hach AL-36 field kit. Water depth, Frazer River temperatures, and weather observations were recorded daily at the fishpass. Water temperatures of tributary spawning areas were recorded throughout the spawning period in conjunction with surveys.

Results and Discussion

Introductions and Adult Returns

Sockeye introductions at Frazer Lake totalled 29 894 transplanted adults, 10 936 000 eggs, and 2 975 000 fry (Table 1). Early sockeye returns from 1956 through 1961 were from the initial green and eyed-egg plants from 1951 through 1956. A combination of adult transplants and natural sockeye spawning between 1961 and 1965 produced the 1965–70 returns. By 1966, the

TABLE 1. Sockeye returns, adult transplants, fry plants, and egg plants at Frazer Lake, 1951–78.

Year	Returns[a]	Adult transplant	Fry plants	Egg plants	
				Eyed	Green
1951–1955	—	0	0	320 000	2 146 000
1956	6	0	0	500 000	0
1957	165	0	0	0	0
1958	71	42	0	0	0
1959	62	0	0	0	0
1960	440	0	0	0	0
1961	273	600	87 000	0	0
1962	1 290	1 800	0	0	0
1963	2 357	9 500	0	0	0
1964	8 166	1 800	0	0	0
1965	5 074	4 000	0	830 000	0
1966	11 728	4 728	504 000	600 000	0
1967	14 500	7 334	0	1 190 000	0
1968	16 708	30	312 000	3 387 000	0
1969	13 981	60	600 000	1 963 000	0
1970	24 039	0	945 000	0	0
1971	55 366	0	527 000	0	0
1972	66 419	0	0	0	0
1973	56 255	0	0	0	0
1974	82 609	0	0	0	0
1975	64 199	0	0	0	0
1976	119 321	0	0	0	0
1977	139 548	0	0	0	0
1978	141 981	0	0	0	0
Total	824 558	29 894	2 975 000	8 790 000	2 146 000

[a]Sockeye counted at the top of the fishpass or back-packed over the falls prior to 1963.

sockeye run had reached the point where potential production from natural spawning exceeded that of the planting effort. As the run became self-sustaining, supplemental introductions were gradually phased out and terminated in 1971. Sockeye continued to increase from the initial return of 500 in 1956 to a record of 141 981 in 1978.

The chinook run, still in an early stage of establishment, was created from plants totalling 160 000 fry over a 4-yr period beginning in 1966 (Table 2). A natural run of chinook salmon did not exist in the Frazer River before the introductions. A total of 555 chinook adults have ascended the fishpass since the first return in 1970. An unknown number of chinook spawn in the river below the fishpass.

The combination of planting methods and natural spawning precludes evaluation of a single method in establishment of sockeye at Frazer Lake. Blackett and Davis (1970) reported eyed sockeye egg to fry survival of 33.5% at Little Kitoi Lake, Afognak Island using the same shovel-cylinder method of planting as at Frazer. Survival of low density sockeye eyed-egg plants to emergent fry at Karluk Lake in 1978 was 11.0% for the planting cylinder method and 50.8% for a hydraulic planter (L. E. White, Alaska Dep. Fish. and Game, unpublished data, 1976). The highest survival of planted fry to smolt in a rehabilitated lake on Afognak Island was 46.9% (Meehan 1966). Five successive fry plants resulted in smolt survivals ranging from 33.4 to 7.3% in an 8-yr period after rehabilitation. The lake was allowed to "rest" without any further planting for 2 yr after the year of final smolt migration and then replanted. Smolt survival from the final fry plant, eleven years after rehabilitation, was 38.8%. (W. R. Meehan, Alaska Dep. Fish. and Game, unpublished data) reported highly variable fry to smolt survivals (0.2–28.3%) for sockeye fry plants in four other lakes on Afognak Island.

The variability in survival of experimental sockeye egg and fry plants in other lakes suggests that the combination of planting methods at Frazer Lake may have increased the probability of success. Fry plants probably had a higher survival to smolt than either egg plants or adult transplants. Plants of less than 60 000 chinook fry a year produced sufficient returning fish to establish this species in the Frazer River. Transplanted sockeye initially attempted to leave the lake and appeared late and in fewer number on spawning areas. The egg to fry survival of transplanted fish that spawned successfully was probably the same as natural returning fish. Egg plant sites in the tributaries of Frazer Lake were occasionally altered overwinter by high flows and

TABLE 2. Chinook salmon introductions and returns to the Frazer Lake fishpass, 1966–78.[a]

Year of plant or return	Fry plants	Adult returns from	
		Planted fry	Natural spawning
1966	42 000		
1967	56 000		
1968	46 000		
1969	16 000		
1970		2	
1971		24	
1972		113	
1973		35	
1974		12	
1975			7
1976			28
1977			208
1978			131

[a]Additional chinook spawn in the Frazer and Dog salmon rivers below the fishpass, but only fish ascending the fishpass are counted.

deposition of sediment. Clusters of dead eggs in these sites indicated either substantial or total mortality. However, the initial egg plants did produce adult returns from 1956 to 1960. Natural spawning of these fish, with the exception of 42 transplanted sockeye, resulted in annual returns of 1290 to 8166 sockeye between 1962 and 1965.

SOCKEYE RETURN PER SPAWNER

Potential egg deposition (PED) and the sockeye return to the Frazer fishpass produced for each parent year (Table 3) is projected from age, sex, and size composition samples and fecundity relationships. Return per spawner, a relative indication of survival, has averaged 3.2 for 7 parent years (1966–1972) in which returns are complete with the exception of two minor age-classes. The highest return was 4.8 for the 1969 parent year and the lowest 2.0 for parent year 1966. Returns from the 1973 parent year are still incomplete and could be increased significantly by fish of the 2.3 age-class in 1979. Data are still insufficient to establish a trend, but a decreasing return per spawner is likely to occur after the 1970 parent year.

Potential sockeye production has increased greatly since 1970. There has been over a sevenfold increase in PED from 1970 to 1978 from natural spawning. The 141 981 sockeye escapement in 1978 is expected to produce a return exceeding 280 000 fish in the 1980s. The return to the fishpass is what remains of the run after the commercial harvest and natural mortality. The fishpass is being expanded by additional steeppass runs to accommodate sockeye escapements of 300 000 to 400 000 projected to occur after 1982.

CONTRIBUTION TO COMMERCIAL FISHERY

The commercial salmon fishery, consisting of set gill nets and purse seining, has not in past years taken a significant portion of the Frazer sockeye run. The timing of sockeye return has been primarily during fishery closures prior to the pink salmon season. However, in future years Frazer sockeye are expected to contribute from 0.3 to 0.6 million sockeye annually to the harvest in an early season fishery in districts on

TABLE 3. Adult sockeye return in relation to parent year escapement and potential egg deposition at Frazer Lake.

Parent						
Year	Escapement[a]	Female spawners	Supplemental[b] production ($\times 10^6$)	Total potential egg deposition ($\times 10^6$)	Return produced	Return/ spawner
1964	9 966	4 983	0	15.2	—	—
1965	9 074	4 628	0.8	14.3	—	—
1966	16 456	8 052	1.1	24.8	33 669[c]	2.05
1967	21 834	11 135	1.2	35.5	86 476	3.96
1968	16 738	9 104	3.7	32.5	59 800	3.57
1969	14 041	7 300	2.6	24.8	68 073	4.85
1970	24 039	11 173	1.0	32.5	73 605	3.06
1971	55 366	28 952	0.5	79.3	123 310	2.23
1972	66 419	30 404	0	87.2	167 599[d]	2.52
1973	56 255	28 953	0	83.2	42 071[e]	0.75
1974	82 609	35 185	0	105.9	—	—
1975	64 199	40 276	0	124.7	—	—
1976	119 300	66 320	0	209.8	—	—
1977	139 548	67 300	0	220.4	—	—
1978	141 981	75 405	0	243.8	—	—

[a]Includes transplanted fish through 1969 as well as adults from natural spawning and egg and fry plants.
[b]Eyed-egg and fry plants in addition to natural egg deposition.
[c]Adult return data for age-class 1.1 (1969) not available.
[d]Incomplete for age-class 3.3 that will return in 1979.
[e]Incomplete for age-classes 2.3, 3.2, and 3.3 that will return in 1979 and 1980.

FIG. 3. Recovery location and migration route of tagged sockeye salmon through fishery districts on the Shelikof Strait side of Kodiak Island.

the West and Southwest side of Kodiak Island. An estimated 36 000 Frazer sockeye were harvested during a June fishery in 1978. A concentrated set gillnet fishery in the Moser–Olga Bay section (Fig. 3), could benefit greatly from this development project. The chinook run will be an additional bonus to commercial and sport fisheries in the area.

The complexity of managing the Frazer sockeye run is evident from sockeye tagging experiments conducted in June 1977 along the Shelikof Strait side of Kodiak Island (Fig. 3). Tagged fish were recovered at weirs on the lake outlets and the Frazer fishpass. Thirty-four percent of the tag recovery was Frazer Lake sockeye which had migrated southwestward along the coast of Kodiak Island in June and early July. If this migration pattern is representative of the majority of Frazer sockeye, there will be mixing with three other sockeye stocks that are also of substantial magnitude in five fishery districts on the westside of Kodiak Island. Management of these mixed stock fisheries, to maintain optimum sockeye escapements at Frazer Lake, will become increasingly difficult as the run develops.

TIMING AND COMPOSITION

Sockeye passage at the fishpass occurs between June 1 and August 31. Peak passage of 60–70% of the annual escapement has typically been concentrated between June 15 and July 15. The sockeye return is nearly complete by early August when pink and chum salmon ascend the fishpass. The developing run of chinook is still too small to determine a peak migration period, but extends from late June through the end of August.

Age composition of Frazer sockeye has consisted of 12 age-classes. Age 1.2, 1.3, 2.1, 2.2, and 2.3 fish have been dominant. Female sockeye comprising 51.7% of the annual escapements from 1965 to 1978, have averaged (±SD) 53.1 ± 2.0 cm and 2.1 ± 0.3 kg. Male sockeye have averaged 52.2 ± 2.4 cm and 2.1 ± 0.3 kg.

Each year, males consistently return to the lake early in the run at about twice the rate of the females. The sex ratio becomes equal during midseason and shifts to a greater number of females during the latter part of the run. An early or late commercial fishery could selectively harvest males or females, alter the natural sex ratio balance, and ultimately decrease sockeye production.

Timing, age, and size of adult sockeye at Frazer is about the same as the Red Lake donor stock. The early run timing at Frazer was created by selecting sockeye from the June escapement at Red Lake for planting. The early run avoids an unmanageable mixed stock and species fishery in Moser–Olga Bay.

Chinook returning to the fishpass have been age 1.1, 1.3, and 1.4. The majority of these fish have spent 3- and 4-yr in saltwater. Length and weight of chinook ($n = 208$) has averaged (±SD) 84.5 ± 4.1 cm and 10.1 ± 1.7 kg for females and 80.2 ± 6.9 cm and 9.1 ± 2.0 kg for males. Sex ratio of 128 chinook sampled in 1977 was 61% male to 39% female.

SPAWNING AREA

In 1975, 64 km of tributary streams and 29 km of lake shore at Frazer Lake were surveyed to evaluate spawning area and quality and estimate capacity for sockeye. Assumptions for estimating capacity were: (1) an optimum density of one female per 2.0 m^2 of area based upon studies at Karluk Lake (Burgner et al. 1969), the closest sockeye system with spawning area of comparable quality; (2) a natural distribution of sockeye spawners over all potential areas to optimum capacity which in reality may seldom be achieved; and (3) an equal sex ratio of spawners in the escapement. Although there is a definite seasonal difference in ratio, the overall sex ratio has been close to equal.

Potential spawning area at Frazer Lake, based upon the assumptions, is 346 905 m^2 with a capacity for supporting 365 000 sockeye spawners. A prespawning mortality of an estimated 5% of the escapement would require an annual escapement goal of 383 000 sockeye. The greatest potential spawning area is the lake shore and the main inlet tributary, Pinnel Creek (Table 4).

The spawning area at Frazer Lake is of equivalent quality to sockeye spawning area in Karluk and Red Lakes. The three lakes have an abundance of tributary springs which maintain water flow, quality, and tem-

TABLE 4. Potential sockeye spawning area and capacity at Frazer Lake.

Spawning area	Potential no/m²	Optimum no. of females
Lakeshore	140 476	70 238
Lateral tributaries	46 309	23 155
Terminal tributary Pinnel Creek (mouth to forks)	67 056	33 528
East Fork Pinnel Creek	62 398	31 199
North Fork Pinnel Creek	35 471	17 736
Frazer River (above falls)	13 195	6 598
Total	364 905	182 454

Optimum number of spawners (both sexes) for available spawning area — 365 000[a]
Estimated prespawning mortality at 5% of escapement — 18 000[a]
Sockeye escapement goal based upon available spawning area — 383 000[a]

[a]Rounded to nearest thousand.

perature regimes throughout the year. Stream gradients and gravel composition are generally similar. Frazer Lake has a greater extent of spawning area than Red Lake, but less than Karluk Lake. Water temperature of spawning areas at Frazer range from about 4 to 15°C during the period of sockeye spawning.

One of the earliest spawning area surveys at Frazer Lake was conducted in July and August of 1964. That year, 2939 sockeye were counted in only three lateral streams and Pinnel Creek after an escapement of 8166 and a transplant of 1800 fish (Meehan et al. 1965). In 1967, spawning in one additional lateral stream and the lake shore (286 sockeye) was recorded for the first time. Spawning of approximately 500 sockeye in a tributary of the Frazer River below the falls in 1967 may have been induced by delayed fish passage. As natural returns increased in the 1970s, there was an extension of spawning range in the original areas as well as utilization of new areas in the lake system. Spawning in the Frazer River tributary ended about 1970, but about 40 sockeye were paired in the lake outlet stream above the falls in 1977.

In 1977 and 1978, eleven lateral tributaries, lake shore, Pinnel Creek terminal tributary, and the Frazer River above the falls were used by sockeye spawners. A total of 59 660 sockeye was counted on spawning areas on a foot survey during the peak period of spawning (July 20–August 20). Of this total, 83.8% were located in the Pinnel Creek tributary system, 9.6% along the lake shore, 6.5% in lateral tributaries, and less than 0.1% in the Frazer River above the falls.

The East Fork of Pinnel Creek which supported the highest density of spawners is also the most extensive area of high quality habitat for spawning in the Frazer system. In 1977, this area was close to, or possibly exceeded the optimum density projection of 62 400 sockeye. The range of spawning has been extended upstream as density of spawners increased. Only about 0.7 km of the upstream portion of this tributary remained unutilized in 1977.

The lake shore has the greatest potential for sockeye spawning, but is still far below capacity. Utilization of lake shore areas is increasing more slowly than in Pinnel Creek. Concentrations of sockeye spawn in an area of upwelling springs close to Midway Creek.

The first observation of redd construction by chinook in the Frazer Lake outlet was on August 17 and 26, 1972. Since 1972, chinook have spawned in the Frazer River both above and below the falls. Spawning areas and concentrations were generally at the same sites as the fry releases with an extension of spawning downstream in the Frazer River in recent years. A foot and float survey in 1977 revealed 140 chinook in the river between the lake and falls. At least 18 of these fish were paired and actively spawning. A minimum of 21 chinook were estimated in a 3.2 km stretch of river below the falls. Returning progeny from natural spawning in the Frazer River is an encouraging indication that chinook have also become successfully established.

One interesting aspect of the Frazer Lake project has been the increasingly greater extension and utilization of new spawning areas as the sockeye run developed over the years. Sockeye undoubtedly have a very complex system of imprinting and homing in order to return to a specific site of hatching in a lake system consisting of many tributaries and often a series of lake sources. The natural extension of spawning into areas in which fry and egg plants were never made at Frazer indicates that a certain amount of straying into new spawning areas also takes place and increases with density of returns. Fry and adult transplants into the lake may have induced a greater degree of within lake straying than releases in a spawning area. Transplanted adults attempting to leave the lake would often remain for one or two weeks in front of the outlet weir before either the urge to spawn or search for their home stream within the lake stimulated movement upstream into spawning areas. Chinook adults, in contrast have tended to return to specific sites in the Frazer Lake outlet above the falls and lower river in which they were released as fry as well as downstream spawning areas below the fishpass.

REARING AREA

The volume of the sockeye rearing area in Frazer Lake, calculated to the 30.5 m depth, is 391 991 310 m³. Russell (1972) showed by echo sounding studies at Frazer that juvenile sockeye rearing in the summer was primarily limited to diurnal movements between the surface at night and a maximum depth of 30.5 m during the day. The capacity of rearing area at Frazer Lake is projected to be sufficient for 60 million sockeye fry. This projection is based upon studies of optimum sockeye fry planting densities in rehabilitated lakes on Afognak Island (Meehan 1966; Blackett et al.

1969) in which a density of 0.153 fry/m^3 of lake area produced the maximum number of smolt. Survival of fry to smolt in Frazer Lake could vary considerably from survival in a rehabilitated lake on Afognak Island. Therefore, the projected density is a preliminary goal that will require further evaluation.

Production of 60 million sockeye fry would require 600 million eggs deposited by 200 000 females in an escapement of 400 000 viable sockeye spawners, assuming that egg deposition to fry survival was 10%, egg deposition averaged 3000 per female, and the sex ratio was equal. To maintain an optimum density of fish in the rearing area, the annual smolt out-migration and freshwater mortality would have to be equivalent to annual fry recruitment. This balance is unlikely. The mortality and number of fish leaving the lake annually is undoubtedly highly variable from year to year.

The escapement of 365 000 sockeye previously projected as the capacity for spawning area is 35 000 fish less than what is required to produce 60 million sockeye fry the rearing area could theoretically support. The relatively small difference between spawning and rearing capacity from natural spawning suggests that supplemental production of sockeye fry at Frazer Lake is not desirable unless rearing capacity or lake productivity can also be increased by lake fertilization or some other method.

The physical characteristics and environmental parameters of Frazer Lake are similar to the Karluk and Red Lake sockeye systems. All of the lakes are oligotrophic with high quality, clear water. Dissolved oxygen, alkalinity, total hardness, free carbon dioxide, and pH of Frazer Lake have ranged from 9–13 mg/L, 14–39 mg/L, 17–51 mg/L, 1.5–25.0 mg/L, and 6.6–7.5, respectively, from June through August. Lake water temperature at the surface in May is normally about 4.5–5.5°C and reaches 12.0–14.0°C by the end of August. A thermocline with a 3.0–4.0°C difference usually develops between the 5 and 20 m depth. Littoral rearing areas for sockeye fry at Frazer Lake are limited to a narrow shoreline that descends rapidly to deep water. Only 9% of total lake volume is above the 3-m contour. The deepest lake depth recorded by Russell (1972) was 59 m. Red and Karluk Lakes have more extensive littoral areas for sockeye fry rearing than Frazer Lake.

Zooplankton, the prime food source of young sockeye, has been sampled at Frazer Lake to indicate changes in abundance and composition that can be correlated with increasing density of sockeye in the nursery rearing area. Even though there has been minor variation in sampling technique since 1965, the results (Table 5) indicate a decrease in zooplankton during the 1970s and a long-term trend of decreasing copepods, increasing cladocerans, and a relatively stable rotifer population. The higher index density in 1977 is partly due to samples collected only during peak blooms in July and early August. Copepods and cladocerans usually increase in number during June and July with peak blooms in August. Rotifer blooms occur in July and some years there may be two or more blooms per year.

The average density of zooplankton in Frazer Lake samples from 1973 to 1976 of 6001 per m^3 is considerably less than the 17 240 per m^3 average for samples taken at Karluk Lake from 1973 to 1975 (L. E. White, Alaska Dep. Fish and Game, unpublished data, 1976). Historically (1927–30), Karluk zooplankton averaged 235 100 per m^3 (Juday et al. 1932) indicating a dramatic decline that coincided with decline of the Karluk sockeye stock. Karluk Lake plankton samples usually contain a higher proportion of rotifers than copepods and cladocerans. An increased nutrient supply from salmon carcasses at Frazer Lake may eventually increase plankton and productivity of the sockeye rearing area.

TABLE 5. Zooplankton density and composition per cubic metre of water at Frazer Lake, 1965–77. Number of organisms is an average of samples taken each summer.

Year	Sample Period	Sample No.	Cladocerans No. (%)	Copepods No. (%)	Rotifers No. (%)	Total no. zooplankton
1965	June 17–Aug. 31	11	275 (2.2)	9730 (78.0)	2467 (19.8)	12 472
1966	May 28–Aug. 22	14	90 (0.8)	9789 (92.3)	724 (6.8)	10 603
1967	May 15–July 27	17	438 (3.1)	9737 (69.9)	3745 (26.9)	13 920
1968	June 11–Aug. 24	17	502 (2.9)	11 985 (69.1)	4849 (28.0)	17 336
1969	—	0	— —	— —	— —	—
1970	May 14–Sept. 31	7	1570 (9.7)	8970 (55.3)	5681 (35.0)	16 221
1971	June 23–Aug. 30	26	166 (4.2)	1655 (42.0)	2115 (53.7)	3936
1972	June 6–Aug. 27	36	228 (3.5)	2611 (40.2)	3649 (56.2)	6488
1973	June 9–July 28	36	430 (12.6)	1895 (55.4)	1094 (32.0)	3419
1974	May 11–Aug. 20	24	867 (9.4)	4250 (46.3)	4066 (44.3)	9183
1975	—	—	— —	— —	— —	—
1976	May 25–Aug. 19	49	1109 (20.5)	2177 (40.3)	2113 (39.1)	5400
1977	July 8–Aug. 6[a]	16	1523 (16.4)	4660 (30.2)	8227 (53.4)	15 410

[a]Samples taken only during the period of peak blooms.

Rearing area of chinook salmon is primarily in the Frazer River or tributaries with the possibility of some lake rearing of fry from outlet spawners. Rearing habits and locations of chinook at Frazer have not been studied due to the recent introduction and natural spawning of this species. Scale samples indicate that the majority of young chinook at Frazer spend one year in freshwater before migrating to sea. A few 2-yr smolt and fish of the year have also been collected. Frazer River from the lake to a short distance below the falls remains open in the winter and lower sections of the river are usually ice-free. Several deep pools in the lower river could provide potential overwinter rearing area for young chinook.

Smolt Outmigration

Sockeye smolt migrate from Frazer Lake to Olga Bay from May through August each year. The peak of migration usually occurs in June. Typically, the older smolt of age-groups 2.0 and 3.0 precede the smaller age 1.0 smolt in the migration. Russell (1972) illustrated the timing sequence by age of Frazer smolt from 1965 to 1970.

In the early years of the Frazer project, when the number of smolt was relatively minor, a sockeye smolt weir was operated in the lake outlet to obtain a yearly count. Smolt counts for 5 yr (1965–70) with the exception of 1969, ranged from 26 549 (1965) to 157 291 (1966). The weir was discontinued after 1970 and only cursory estimates of the number of smolt have been recorded since 1970. Smolt outmigrations are estimated to be in "the millions" for the last several years based upon observations of mass concentrations of smolt below the Frazer falls.

The majority of young sockeye leave Frazer Lake at age 1 and 2. A lesser number leave as age 3 fish and a few migrate before the first winter. There has been year-to-year variability in the ratio of age 1 and 2 smolt (Table 6) which is also evident in age composition of adult returns. Since 1973, the majority of adult sockeye have smolted at age 2 while from 1970 through 1973 the returns were primarily from age 1 smolt. Freshwater age of adults, however, does not necessarily represent dominant age groups of smolt. Marine mortality may at times be selective of smolt of a given age. For example, Williams (1969) has shown a highly positive correlation ($r = 0.935$) of increased marine survival of smolt with increased discharge of the Chilko River. If this was also true for the Frazer River, a high discharge early in the migration would favor the older and larger smolt and the younger and smaller smolt if a high discharge occurred late in the migration.

Frazer Lake sockeye smolt are larger than smolt from Karluk, Akalura, or Red lakes. Age 1, 2, and 3 smolt from these lakes have averaged about 84–107 mm (5–12 g), 97–119 mm (7–16 g), and 130–141 mm (20–23 g), respectively, for years of sampling. In comparison, the average size of Frazer smolt in the last 13-yr has ranged from 120–163 mm and 16–36 g for age 1, 142–185 mm and 26–62 g for age 2, and 151–201 mm and 30–76 g for age 3. There has been a decrease in smolt size since the 1960s, but in recent years (1975–77) size appears to have stabilized. The excellent condition and large size of Frazer smolt reflects favorably upon the capability of Frazer Lake to support sockeye introduced into the system. A decrease in smolt size is expected as the sockeye run increases and the capacity of the rearing area is approached.

Freshwater survival of sockeye from egg deposition to smolt at Frazer Lake was evaluated for two parent years (1963 and 1964) in which only transplanted fish supplemented natural escapement and counts of smolts produced are complete. For each of these parent years, 1963 and 1964, respectively, freshwater survival (eggs to smolt) from potential egg deposition (PED) was 0.80% and 0.61% and from actual egg deposition estimate (AEDE) 6.00% and 4.39% (Table 7).

The AEDE calculation for Frazer is based upon a

Table 6. Summary of smolt outmigration and age composition at Frazer Lake, 1965–70 (Reproduced from Russell 1972).

Year of smolt outmigration	Total number smolts	Age			
		0.0	1.0	2.0	3.0
1965	26 945	43 (0.2%)	20 432 (75.8%)	6327 (23.5%)	143 (0.5%)
1966	157 291	31 (0.02%)	36 273 (23.1%)	118 832 (75.5%)	2155 (1.4%)
1967	134 123	0	73 634 (54.9%)	55 674 (41.5%)	4815 (3.6%)
1968	93 793	0	80 212 (85.5%)	13 253 (14.1%)	328 (0.4%)
1969[a]	—	—	—	—	—
1970	44 808	10 (0.02%)	30 500 (68.1%)	14 150 (31.6%)	148 (0.3%)

[a]Weir inoperable due to high water conditions.

TABLE 7. Freshwater survival of Frazer Lake sockeye from egg deposition to smolt for two parent years.

	Parent years	
	1963	1964
No. returning sockeye	2357	8166
No. transplanted sockeye	9500	1800
Estimated number of females	5928	4983
Potential egg deposition (PED) $\times 10^6$	18.0	15.2
Actual egg deposition estimate[a] (AEDE) $\times 10^6$	2.4	2.1
Smolts produced:		
1.0	20 432	36 273
2.0	118 832	55 674
3.0	4815	328
Total	144 079	92 275
Estimated egg to smolt survival from:		
PED	0.80%	0.61%
AEDE	6.00%	4.39%
Smolt per female	24.3	18.5

[a]AEDE is based upon mean PED to AEDE survival at Grassy Point Creek, Karluk Lake from 1964 to 1968 (Drucker 1970).

5-yr study of sockeye egg to fry survival at Grassy Point Creek, Karluk Lake (Drucker 1970) in which hydraulic sampling provided a means of assessing the difference between PED and AEDE as well as fry survival. The percent of live eggs remaining between PED and AEDE in the Karluk study ranged from 3.0 to 23.3% with an average of 13.6%. PED to fry survival ranged from 1.45 to 11.53% (average of 4.65%) and from AEDE, 19.00 to 42.83% (average of 28.97%). The great loss of eggs between PED and AEDE at Grassy Point Creek was attributed by Drucker to predation by bears which probably is not as great a factor for most spawning areas at Frazer Lake.

Chinook smolt have been sampled in the Frazer Lake outlet incidental to sockeye smolt sampling in June. In 1974, 48 chinook smolt ranged in size from 78 mm and 4.9 g to 133 mm and 25.6 g ($\bar{x} \pm SD = 106.4 \pm 11.5$ mm and 13.2 ± 4.6 g). Twenty-two chinook smolt in 1975 ranged from 61 mm and 3.1 g to 115 mm and 14.4 g ($\bar{x} \pm SD = 96.6 \pm 10.1$ mm and 9.9 ± 3.5 g). All of the chinook were age 1 and appeared to be healthy and robust fish.

General Discussion

Successful establishment of sockeye and chinook stocks at Frazer Lake is attributed to the following factors: (1) initiation of an ambitious program of salmon introductions and fish passage enhancement that was continued until natural returns and production was sufficient to maintain viability; (2) selection of donor stocks from nearby systems (Karluk and Red Lakes) that closely matched environmental and biological parameters of Frazer Lake; (3) use of a combination of planting methods which assured a greater degree of success than a single method alone; and (4) a highly favorable environment at Frazer Lake to produce and support sockeye and chinook runs which could not have developed naturally due to a barrier falls in the lake outlet.

Perhaps the most extensive history of sockeye egg, fry, and adult transplantation to produce salmon runs that is relevant to the Frazer Lake project, is that of the International Pacific Salmon Fisheries Commission (IPSFC) on the Fraser River system in British Columbia, Canada. In over 18 transplants from 1950 to 1960 of a combined total of 10.4 million eyed eggs, only about 23 000 adult sockeye were documented as returning (IPSFC, 1954–64) and only 11 of the transplants were known to produce fish. Of these, only the Portage Creek plants showed promising results with returns of about 20 000 adults. Returns to other recipient systems varied from 1 to 499 fish.

Transplants of 292 000 fingerling sockeye in 1950 were also unsuccessful, although an experimental plant in which eggs were taken from Horsefly Lake spawners, incubated at a hatchery on the lake, and 94 000 fingerlings released at the river mouth produced a return of 1177 adults (1.25% survival) to the hatchery and adjacent river, but not to the spawning area of the parents (IPSFC 1954). Plants of 7.0 million sockeye fry into Horsefly Lake were unsuccessful in creating a run due to the fish remaining in the lake. Only 25 053 smolts were produced (IPSFC 1960).

An adult sockeye transplant of 1000 fish from downstream spawning areas to potential spawning area above a falls in Horsefly River failed because all of the fish dropped back over the falls to the original spawning area. However, when 749 adult sockeye were transplanted from the river to artificial spawning grounds, egg deposition success was 59–76% in densely populated sections (1.0 female per m^2) and 78 to 92% at 1.0 female per 1.5 to 5.7 m^2 (IPSFC 1958).

In the early 1960s the Commission recognized the highly variable results of their rehabilitation efforts on the Fraser River system:

> "Hatcheries of the Fraser River were closed by the Federal Government in 1937 because they had been proven to be economically unsound where they were competitive with natural spawning areas. Many attempts had been made to transplant runs from one area to another, but there was no recorded instance of a run being transplanted that was capable of maintaining itself by natural propagation" (IPSFC 1961). "The entire history of artificial propagation and transplantation of sockeye has been associated with many unexplained failures and the occasional and rather remarkable though unexplained success in areas other than the Fraser River watershed" (IPSFC 1964).

Many of the traditional hatchery concepts for salmon rehabilitation and enhancement did not produce satis-

factory results. New methods of egg and fry incubation using substrate incubators, upwelling flow channels, spawning channels, and fry rearing, were developed on the Pacific Coast after the mid-1960s. Additionally, incubation systems developed from small experimental units into production systems with the capability by massive plants of fry or eyed eggs to overcome high mortality in various phases of sockeye life history. Substantial adult returns could be gained in the first 5- or 6-yr cycle rather than 20- to 25-yr, as for the Frazer Project.

Canada invested in the construction of spawning channels on the Fraser and Babine systems to meet their enhancement goals. The six channels operated by the Commission on the Fraser River have been highly successful (Cooper 1977), while channels contributing fry to Babine Lake, although also successful, have experienced some biological and operational problems. The Commission in recent years has also continued plants of eyed sockeye eggs. Eggs transplanted to the Upper Adams River in 1974 produced 95 000 smolts in 1975 (6.9% eyed-egg to smolt survival). An additional 2.1 million eggs planted in 1975 could result in sufficient adult returns to begin reestablishment of what was once a large run to this river (IPSFC 1976–1977).

The Lake Washington sockeye run is perhaps the only other successful introduction on the Pacific Coast to result in a viable stock. Young sockeye were introduced into the Cedar River in 1936. Returns were insignificant until about 1958 when 15 000–20 000 spawners returned to the river. By 1960, the escapement was 24 000, then declined for several years until 1964 when 68 500 spawners were counted at the weir. An escapement of about 200 000 (estimated catch of 70 000) sockeye in 1969 was a fourfold increase over the 1965 parent year (Washington State Department of Fisheries 1970).

Considerable effort and experimentation has been conducted to introduce or reestablish sockeye in lake systems on the Pacific Coast. Success in actually developing self-sustaining salmon stocks, however, has been extremely limited. Establishment of sockeye and chinook at Frazer Lake is the only known instance on the Pacific Coast where introductions have resulted in a major salmon run in a system where salmon were previously nonexistent and the lake inaccessible. The successful development of this project is especially encouraging and stimulating when natural salmon populations have undergone long-term declines prompting the State of Alaska to initiate a large scale salmon rehabilitation and enhancement program.

Future success of the Frazer salmon runs and achievement of optimum production that could result in returns of 0.7–1.0 million sockeye annually will depend in part on the ability to manage the harvest in what will be, in all likelihood, a very complex mixed stock fishery. Perpetuation of this unique run will depend upon long-term evaluation and an effective management strategy.

Acknowledgments

Many people, too numerous to mention, have contributed over the last 28 yr to the Frazer Lake enhancement project. Their successful efforts are fully acknowledged. Special recognition is extended to Mr Clint Stockley who had the foresight to recognize the potential of Frazer Lake and make the first egg plants in 1951. The Alaska Department of Fish and Game (Department of Fisheries prior to 1957) believed firmly from the beginning in the success that could be achieved by salmon introductions into Frazer Lake and in spite of initial controversy then, as there would be today, successfully established a salmon run that is unique in the history of salmon fisheries.

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Influence of Age, Condition, Sampling Time, and Method on Plasma Chemical Constituents in Free-Ranging Ringed Seals, *Phoca hispida*

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Blood samples were obtained from 29 free-ranging ringed seals, *Phoca hispida*, on Herschel Island, Y.T.; 10 were shot and 19 were caught in nets. Age, condition, sampling time, and method had variable influence on plasma chemical constituents. Plasma sodium, chloride, and cholesterol levels in three seals judged to be in poor condition were lower than in the 26 remaining seals. Uric acid was highest in shot pups, but the dynamics of this nitrogenous metabolite in seals are obscure. Plasma levels of alkaline phosphatase, calcium, and cholesterol varied with age. Shot seals had higher plasma triglycerides and blood urea nitrogen (BUN), as a result of recent feeding. For reasons unknown, the circulating levels of two hepatocellular enzymes were elevated in all samples. Plasma from shot seals had falsely elevated potassium levels, due to the sampling technique. Glucose, bilirubin, inorganic phosphate, and aspartate aminotransferase were not significantly influenced by any of the variables studied. The plasma electrolytes and BUN in five captive ringed seals sampled over a 1-yr period correlated with levels in healthy, fasted free-ranging seals; uric acid levels were lower in the captive seals.

Key words: phocid, ringed seals, plasma chemistry, hyponatremia, uric acid, enzymes

GERACI, J. R., D. J. ST. AUBIN, AND T. G. SMITH. 1979. Influence of age, condition, sampling time, and method on plasma chemical constituents in free-ranging ringed seals, *Phoca hispida*. J. Fish. Res. Board Can. 36: 1278–1282.

Les auteurs ont prélevé des échantillons de sang sur 29 phoques annelés, *Phoca hispida*, en liberté dans l'ile Herschel, T. Y.; 10 avaient été tués au fusil et 19 capturés dans des filets. Age, état d'embonpoint, époque et méthode d'échantillonnage exercent une influence variable sur les constituants chimiques du plasma. Les concentrations de sodium, chlorures et cholestérol plasmatiques chez trois phoques considérés comme étant en pauvre état sont plus faibles que celles des 26 autres phoques. L'acide urique est à son maximum chez des chiots tués au fusil, mais la dynamique de ce métabolite azoté chez les phoques est mal connu. Les niveaux d'alcaline phosphatase, calcium et cholestérol dans le plasma varient en fonction de l'âge. Les phoques tués au fusil contiennent plus de triglycérides plasmatiques et d'azote de l'urée sanguine (BUN), par suite d'une alimentation récente. Pour des raisons inconnues, les niveaux de deux enzymes heptacellulaires circulantes sont élevés dans tous les échantillons. La méthode d'échantillonnage produit chez les phoques tués au fusil des niveaux de potassium plasmatique faussement élevés. Glucose, bilirubine, phosphate inorganique et aspartate aminotransférase ne sont pas affectés de façon appréciable par aucune des variables étudiées. Les électrolytes plasmatiques et le BUN de cinq phoques annelés maintenus en captivité et échantillonnés sur une période d'un an sont en corrélation avec les concentrations trouvées chez des phoques libres, à jeun et en bonne santé; les niveaux d'acide urique sont plus bas chez les phoques en captivité.

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BLOOD plasma is a dynamic medium: it is readily available, it changes with relation to the physiological status of an animal, and it is a sensitive index of condition. With automated equipment, plasma can be analyzed swiftly and economically, thus making it practical to acquire chemical profiles on a wide range of animals. For pinnipeds, this has spawned considerable data. There has been, however, little attempt to correlate such features as age, condition, sampling time after capture, and blood collection technique with subtle but important differences in findings (Kooyman and Drabek 1968; Seal et al. 1971).

This study demonstrates the nature and extent of some of these differences in one pinniped species, the ringed seal, *Phoca hispida*. Much of the field study was carried out in 1971, but our findings have only recently been interpreted in the light of information subsequently gained from captive animals.

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Materials and Methods

As part of a tag and release program on Herschel Island, Yukon Territory, 19 ringed seals were netted during the summer of 1971 (Smith et al. 1973). These included six 4–5-mo-old pups (2 ♂, 4 ♀), one yearling (♂), one 4-yr and one 5-yr class seal (2 ♀), and 10 adults (6 ♂, 4 ♀) aged 6–8 yr. Ages were estimated by counting the ridges on the claws of the foreflippers (McLaren 1958). After capture, the seals were placed in a dry wooden enclosure within 100 m of the capture site, where they remained until sampled for blood, tagged, and released within 24 h. Blood was drawn from the pelvic flipper (Geraci 1971), or the extradural intravertebral vein (Geraci and Smith 1975).

Blood samples also were obtained from 10 seals shot by local hunters. There were eight 4–5-mo-old pups (4 ♂, 4 ♀), and two adults (2 ♀). Only one adult was aged (Smith 1973) and found to be 14+ yr. Blood was taken from the heart, brachial vessels, or free-flowing head wounds, within 1–3 min after death.

Blood was placed in heparinized Vacutainer tubes (Becton, Dickinson and Co., Columbus, Ohio), centrifuged, and separated immediately after sampling. Plasma samples were removed to chemically clean tubes, held at 0–2°C for up to 3 wk, then shipped by air to Montreal where they were analyzed in the biochemistry laboratories of the Hôpital Notre Dame. This storage interval has been shown to have no significant effect on the plasma constituents analyzed (Juul 1967; Hanok and Kuo 1968). The plasma samples were analyzed using multichannel autoanalyzers (Technicon Instruments Corp., Ardley, N.Y.) according to the manufacturer's methodology. Alanine aminotransferase (AlAT) was assayed manually using a Dade enzyme kit (Dade Division, American Hospital Supply Corp., Miami, Fla.). Activities of AlAT and aspartate aminotransferase (AspAT) are reported in Reitman Frankel (RF) units, and alkaline phosphatase (ALP) in King–Armstrong (KA) units. One RF unit represents the formation of 4.82×10^{-4} μmol of glutamate/min at 25°C, and one KA unit of ALP activity liberates 1 mg phenol/30 min at 37°C.

Statistical comparisons of each plasma chemical constituent were made between shot and netted seals (all age-classes), pups and older seals (irrespective of capture method), and pups and older seals within each capture/sampling method. Comparisons were made using the Fisher-Behrens modified t test for unequal variances.

Five captive ringed seals were used for comparative evaluation of eletcrolytes, BUN, and uric acid. They were obtained as pups or subadults from Cape Parry, N.W.T. during September 1974. The seals were transported by air to the University of Guelph where they were maintained in fiberglass pools measuring $2.1 \times 3.0 \times 1.8$ m, and containing 9900 L of filtered water to which was added sodium chloride at a level of 20 g/L. The seals were fed herring, *Clupea harengus*, and smelt, *Osmerus mordax*, and were in apparent good health throughout the study period. After 2 mo of acclimatization, blood samples were collected at approximately 6-wk intervals for 1 yr. Blood was sampled as previously described, from seals fasted 24 h. The heparinized plasma was removed after centrifugation, generally within 1 h of collection. Captive seal plasma was analyzed for sodium and potassium using a Model 143 flame photometer (Instrumentation Laboratory Inc., Boston, Mass.); chlorides were determined with a Buchler-Cotlove chloridometer (Buchler Instruments, Fort Lee, N.J.). Blood urea nitrogen was analyzed by the method of Crocker (1967) and uric acid according to Henry et al. (1957).

TABLE 1. Plasma constituents in wild ringed seals, *Phoca hispida*, in relation to condition: Good = 26 normal seals; Poor = 3 late molting, thin and lethargic seals. (***$P < 0.001$.)

Constituent	Condition		
	Good $\bar{x} \pm$ SD		Poor $\bar{x}$ (range)
sodium (mmol/L)	157±6	***	143 (140–144)
chloride (mmol/L)	104±3	***	97 (95–100)
cholesterol (mg/dL)	299±54	***	218 (198–246)

Results and Discussion

Age, condition, method of capture, and sampling time significantly influenced levels of certain plasma chemical constituents; sex and blood sampling site (6 extradural, 13 flipper) had no effect. Elucidation of these differences was complicated in some instances by age biases in the sample. Shot seals were predominantly pups, while the netted seals were principally 1-yr of age or older. Nevertheless, it was possible to break the sample into subgroups of shot pups ($n = 8$), netted pups ($n = 6$), and netted older seals ($n = 13$), for statistical comparison.

Some of the observed influences on plasma chemical constituents provide significant insights into normal and aberrant physiology in seals, particularly the relationship between chronic stress and electrolyte balance. There was a difference in sodium and chloride levels between the 26 seals in good condition, and three pups judged to be less healthy on the basis of incomplete or late molt, inadequate weight, and general inactive behavior (Table 1). The sodium levels of the latter seals ranged between 140 and 144 mmol/L, compared with 154 ± 3 mmol/L for healthy captive seals (Table 2) and 157 ± 6 mmol/L for free-ranging seals in good condition. Chlorides were similarly depressed (95–100 mmol/L from a normal of 104 ± 3 mmol/L), but were within the range observed in captive seals. Seals in poor condition also had lower cholesterol levels than did the other pups.

Hyponatremia, or low blood sodium, is a pathologic condition of captive phocid and otariid seals. Hubbard

TABLE 2. Plasma chemistry values in five captive ringed seals, *Phoca hispida*, sampled during a 1-yr period.

Constituent	n	$\bar{x} \pm$ SD	Range
Sodium (mmol/L)	38	154±3	149–166
Potassium (mmol/L)	38	4.3±0.4	3.4–5.4
Chloride (mmol/L)	29	102±6	84–112
BUN (mg/dL)	29	39±9	29–57
Uric Acid (mg/dL)	37	1.2±0.4	0.5–2.6

TABLE 3. Plasma constituents in 10 shot and 19 netted free-ranging ringed seals, *Phoca hispida*. (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.)

Constituent	Shot $\bar{x} \pm$ SD	Netted $\bar{x} \pm$ SD	P
Uric acid (mg/dL)	5.4±1.7	2.3±0.6	***
Triglycerides (mg/dL)	344±113	52±11[a]	***
BUN (mg/dL)	54±10	42±12	**
Glucose (mg/dL)	123±22	146±32	*
AlAT (RF-U/mL)	70±33[b]	113±71[a]	*
Potassium (mmol/L)	5.6±1.0	4.2±0.6	**

[a]$n = 17$.
[b]$n = 9$.

TABLE 4. Plasma constituents in free-ranging ringed seals, *Phoca hispida*, in relation to age ($n = 14$ pups, 15 adults).

Constituent	Pup $\bar{x} \pm$ SD	Adult[a] $\bar{x} \pm$ SD	P
Uric acid (mg/dL)	4.4±1.7	2.3±1.3	***
Triglycerides (mg/dL)	235±178[b]	90±100[c]	*
Glucose (mg/dL)	124±31	151±25	*
AlP (KA-U/mL)	6.3±3.3	3.0±0.6	**
Potassium (mmol/L)	5.2±1.2	4.2±0.5	**
Calcium (mg/dL)	9.4±0.9	8.7±0.5	*
Cholesterol (mg/dL)	260±47	320±51	**

[a]All seals 1 yr or older.
[b]$n = 13$.
[c]$n = 14$.

(1968) first observed the condition, and related it to freshwater captivity. Since then, it has been found associated with thiamin deficiency (Geraci 1972), vitamin E deprivation (Engelhardt and Geraci 1978), nonspecific stress (Geraci 1972) and diets of poor quality fish (Geraci 1975). The cause of the condition is unknown; it may be related to, but is not entirely, a syndrome of adrenal–cortical insufficiency. In both its biochemical nature and response to therapy, hyponatremia appears to be the result of a defect in aldosterone production by the zona glomerulosa (Geraci 1972).

The finding of hyponatremia in wild unhealthy ringed seals is indeed fortuitous. It dismisses or at least weakens the suggestion that the syndrome is associated only with a freshwater environment, and reaffirms the relationship between hyponatremia and disease or stress-related adrenal dysfunction. Above all, it establishes the condition in free-ranging animals, and suggests that the surprisingly low limit of "normal" sodium which Kooyman and Drabek (1968) reported for free-ranging Weddell seals, *Leptonychotes weddelli* (146 ± 6.4 mmol/L, range 132–155 mmol/L) may signal the occurrence of hyponatremia in that species as well.

Uric acid levels in seals are difficult to interpret, and this study proved to be no exception. Shot seals had significantly higher levels than netted seals (5.4 ± 1.7 mg/dL vs. 2.3 ± 0.6 mg/dL, $P < 0.001$ (Table 3). The shot seals were principally pups, and the apparent differences between pup and adult uric acid levels (Table 4) is due to this sampling bias. Analysis of uric acid levels within each age sample shows that shot pups had significantly higher uric acid levels than netted pups (5.7 ± 1.2 mg/dL vs. 2.7 ± 0.7 mg/dL, $P < 0.001$), whereas no differences were noted between netted pups (2.7 ± 0.7 mg/dL), and netted adults (2.0 ± 0.4 mg/dL).

The reason for higher uric acid levels in shot seals is obscure. Using harp seals, *Phoca groenlandica*, we tested the possibility that this may have been due to recent feeding. We found no correlation between postprandial status and uric acid levels (Geraci and St. Aubin unpublished data).

Uric acid can be influenced by at least some forms of stress in ringed seals. In a separate study, three subadult ringed seals were placed in oil-covered water, after having been in captivity for 2 mo. Within 71 min of the obviously stressful episode, plasma uric acid showed an increase from a mean of 3.4 to 5.6 mg/dL (Geraci and Smith 1976). By contrast, the netted seals in this study, which exhibited hematological evidence of short-term capture-related stress (Geraci and Smith 1975), had lower uric acid levels than the shot seals, which were unsuspecting and presumably normal. Consistent with this observation, our laboratory ringed seals had the lowest uric acid levels (1.2 ± 0.1 mg/dL) (Table 2) despite biochemical and histological indication of chronic adrenal cortical stress.

Although age did not influence plasma uric acid in this study, one of us (JRG) has found age-related differences between fasting, recently weaned pups and adult harp seals (*P. groenlandica*) which had levels of 1.6 ± 0.6 mg/dL ($n = 21$) and 0.9 ± 0.3 mg/dL ($n = 15$) respectively. A similar but more modest trend has also been found in the Weddell seal (Seal et al. 1971).

The significance of circulating uric acid levels in mammals is obscure (Kronfeld and Medway 1969). Uric acid is an efficient nitrogen metabolite in terms of water balance, and it may be argued that, as in lower vertebrates (Campbell 1973), a shift to uric acid excretion in pinnipeds would be useful at times when water is not freely available, or in periods of negative nitrogen balance, i.e. during fasting, and when eating high protein, low fat diets (Geraci 1975). This is supported by a single observation of an unusually high value in a captive elephant seal, *Mirounga angustirostris*. Following 8 months of progressive starvation with muscle wasting, plasma uric acid rose to 11 mg/dL (Geraci unpublished data), possibly reflecting increased nucleic acid catabolism. However, the exact nature of these changes is unclear, as are the contrasting findings between and within seal populations. The dynamics of uric acid metabolism in phocid seals present a potentially fascinating study.

Triglyceride levels were higher ($P < 0.001$) in the

shot seals (344 ± 113 mg/dL) than in the netted (52 ± 11 mg/dL) seals. There was also an apparent difference in triglyceride levels between pups and adults (Table 4). However, as in the case of uric acid, this was due to the sampling bias which favored pups in the shot seal group.

The high level of triglycerides in the shot seals can be interpreted simply. They had food remains in their stomachs, and cream colored or lipemic plasma, which is characteristically high in triglycerides (Zilversmit 1965), and points to recent feeding (Nelson 1970). By contrast, the netted animals were held without food for 8 h or more before being sampled. Their plasma was clear, and contained low triglyceride levels. Thus, differences in triglycerides were due to the interval between feeding and blood sampling.

Blood urea nitrogen (BUN) levels can be interpreted similarly on the basis of feeding. The BUN of the shot seals (54 ± 10 mg/dL) was higher than that of the netted seals (42 ± 12 mg/dL, $P < 0.01$) (Table 3). Blood urea nitrogen rises after feeding due to deamination of amino acids (Street et al. 1968), and so the netted animals, fasted before sampling, would be expected to have lower values. This relationship in seals is further reinforced by two observations. Our Guelph captive seals, which are sampled routinely after a 24 h fast, have BUN in the same range as the netted group (Table 2). Also, postprandial harp seals show a steady increase in BUN from 24 to 68 mg/dL over a 9-h period after feeding (Geraci and St. Aubin unpublished data).

The BUN levels in ringed seals are higher than in terrestrial mammals. This is consistent with findings in other phocid seals (Greenwood et al. 1971; Hubbard 1968) and marine mammals generally (Ridgway 1972). The reason for this is unknown, as is the general nature of nitrogen metabolism in these animals. Seal et al. (1971) found age-related differences in BUN of Weddell seals, *L. weddelli* (higher levels in young seals), that were not apparent in this study.

The slight differences in glucose between shot and netted seals and between pups and older seals probably bear no biological significance (Tables 3 and 4). There were no age-related differences in glucose within the sample of netted seals, nor were there significant differences between shot and netted pups. Blood glucose levels in marine mammals are generally higher than those in terrestrial mammals (Medway and Geraci 1965; Kaneko and Cornelius 1970; Ridgway 1972), and are widely influenced by physiological demands (Hochachka et al. 1977). Stress, fasting, and recent feeding are known to affect glucose levels, but the interaction of these factors with other variables cannot be assessed with certainty.

Alkaline phosphatase was significantly higher in pups than in adults (Table 3). This is consistent with findings in other mammalian species, and probably reflects enzyme activity associated with bone development in growing animals (Doxey 1971). There was no concomitant age-related difference in plasma inorganic phosphate; this is unclear in view of the fact that the young of domestic species have levels 3 mg/dL higher than do adults (Kronfeld and Medway 1969).

Plasma levels of alanine aminotransferase (AlAT) were higher in netted than in shot seals (all age-classes) (Table 3). Since there was no difference between levels in shot (75 ± 35 RF-U/mL) and netted (113 ± 105 RF-U/mL) pups, the finding is not considered biologically significant. Both AlAT and aspartate aminotransferase (AspAT) were elevated beyond levels reported for captive ringed seals (St. Aubin and Geraci 1977), gray seals, *Halichoerus grypus* (Greenwood et al. 1971), and northern fur seals, *Callorhinus ursinus* (Hunter and Madin 1976). Notwithstanding differences in analytical procedures, these values would be considered pathological. The enzymes AlAT and AspAT are principally hepatocellular in ringed seals (St. Aubin and Geraci 1977). Elevations in plasma levels generally reflect tissue destruction, but also can be due to stress, exercise and nutritional status (Altland and Highman 1961; Bolter and Critz 1974). There was no significant correlation between plasma AlAT and AspAT levels in this study.

Higher potassium levels in the shot seals (Table 3) were likely the result of blood collection technique. These samples were often crudely obtained from free-flowing head wounds, and from the brachial vessels exposed by cutting through the axillae. Plasma collected in this way seems to have contained enough potassium leached from tissues and lysed red cells (Eadie and Kirk 1952) to yield erroneous results. The netted seals more accurately reflect the normal range of circulating potassium (4.2 ± 0.6 mmol/L), as supported by our findings on the Guelph captive population (Table 2), which over a period of 1 yr showed values (4.3 ± 0.4 mmol/L) nearly identical to those of the netted seals.

Calcium values were slightly lower in the older seals, than in the pups (8.7 ± 0.5 mg/dL vs. 9.4 ± 0.9 mg, $P < 0.05$) (Table 4). These levels are, in fact, lower than those reported for other pinnipeds (Greenwood et al. 1971; Hunter and Madin 1976) and mammals generally (Kronfeld and Medway 1969).

Bilirubin, inorganic phosphate and AspAT were found not to be influenced by age, condition, sampling time or method. The composite data for the population were as follows:

Constituent	n	$\bar{x}$ ± SD (range)
inorganic phosphate (mg/dL)	29	6.0 ± 1.8 (3.4–9.8)
bilirubin (mg/dL)	29	0.4 ± 0.1 (0.1–0.7)
AspAT (RF-U/mL)	27	248 ± 138 (77–561)

This study exemplifies the need to interpret blood findings in free-ranging pinnipeds with reference to certain features of life history, known changes during experimental manipulation, and naturally occurring disorders. It establishes reference values which are a necessary adjunct to husbandry programs for captive phocids,

and it provides insights into biochemical peculiarities in pinnipeds, such as hyponatremia and the obscure but dynamic nature of nitrogen metabolites. Information so gained will provide more sensitive indicators for assessing condition and status of both free-ranging and captive species.

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External Morphology of the Pink Salmon, *Oncorhynchus gorbuscha*, Introduced into Lake Superior

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BERG, R. E. 1979. External morphology of the pink salmon, *Oncorhynchus gorbuscha*, introduced into Lake Superior. J. Fish. Res. Board Can. 36: 1283–1287.

Meristic and morphometric measurements were taken from 33 male and 44 female mature pink salmon, *Oncorhynchus gorbuscha*, collected in three Lake Superior tributaries in Marquette County, Michigan. Significant sexual differences were found for eight characteristics in males and two in females. The male fish had a greater degree of differentiation in the head and hump regions; females had larger and longer anal fins. The Lake Superior fish were found to have shorter bodies, larger and longer fins, and more exaggerated development in the male head and hump than has been reported for the Pacific populations.

Key words: pink salmon, salmonids, exotic species, Lake Superior, morphology

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Les caractères numériques et morphométriques de 33 saumons roses, *Oncorhynchus gorbuscha*, mâles et de 44 femelles matures capturés dans trois tributaires du lac Supérieur, dans le comté de Marquette, Michigan, ont été déterminés. On a trouvé des différences sexuelles significatives avec huit caractéristiques chez les mâles et deux chez les femelles. Les mâles montrent un plus haut degré de différenciation dans les régions de la tête et de la bosse; les femelles ont des nageoires anales plus grosses et plus longues. On constate que les poissons du lac Supérieur ont un corps plus court, des nageoires plus grosses et plus longues et, chez les mâles, développement plus exagéré de la tête et de la bosse que les populations du Pacifique.

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PINK salmon, *Oncorhynchus gorbuscha*, were first recorded in Lake Superior in 1959, following a 1956 accidental introduction of 1955 broodyear Skeena River, B.C. stock from the Port Arthur Hatchery at Thunder Bay, Ontario (Schumacher and Eddy 1960; Scott and Crossman 1973). Scott and Crossman (1973) state that about 21 000 fingerlings were released. It is now apparent that pink salmon have successfully reproduced in the freshwaters of the lake and increasing numbers of adults run up various tributaries to spawn (Scott and Crossman 1973; Eddy and Underhill 1974, Berg 1976).

There are eight distinct spawning populations of pink salmon in Pacific waters. These are the East Kamchatka, West Kamchatka, Okhotsk, Amur, Maritime Province, West Sakhalin, and East Sakhalin in Soviet waters (Eniutina 1954) and the Kodiak-Cook inlet morphotype (Amos et al. 1963) which includes Alaskan and British Columbia (Skeena River) groups. Morphological characters have been analyzed for most of these populations, but little is known concerning meristic characteristics of the exotic Lake Superior population. The purpose of this paper is to determine the range of external meristic and morphometric characters and sexual variability for adult pink salmon in Lake Superior and compare the results to previous Pacific studies.

Materials and Methods

The sampling areas were located in Marquette County in the Upper Peninsula of Michigan along the southern shore of Lake Superior. I collected pink salmon in the Dead River on September 10 and September 13–14, 1975 using a 30 m long, 63.5-mm mesh gill net and in the Laughing Whitefish River on September 16, 1975 using a 325-V D.C. backpack shocker. An additional sample was collected by personnel from the Marquette Fisheries Research Station, Michigan Department of Natural Resources, in the Little Garlic River on September 17, 1975 with similar shockers. The combined collections consisted of 33 males (286–373 mm standard length) and 44 females (296–343 mm standard length) that were in spawning condition and full maturity.

I took meristic and morphometric measurements following methods in Ricker (1971) on fresh samples to prevent any specimen shrinkage. Because of the deterioration of the sample and lack of a preservation method that would not cause body distortion, internal examinations were not attempted. Scale samples were taken for later analysis. After the measurements were recorded, sexual differences in the range of each character were tested with a one-

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TABLE 1. Multiple Wilcoxon two-sample rank sum (Brown and Hollander 1977) test results for those meristic and morphometric characters that indicate significant sexual differences between the sexes of adult Lake Superior pink salmon (critical level = 0.005). Means and standard deviations in millimetres are presented for both sexes.

Character	Males	Females
Lateral line scales	168.1±15.7	155.5±7.2
Snout length	26.7±3.5	20.7±2.4
Head length	85.7±8.4	75.7±5.3
Maxillary bone length	33.4±4.2	28.7±3.3
Lower jaw length	58.4±6.3	46.7±2.2
Body depth	93.5±12.2	79.4±7.1
Dorsal fin height	43.1±5.0	38.3±3.3
Anal fin length	33.2±4.4	41.4±3.4
Anal fin height	32.8±4.3	41.4±3.4
Caudal fin length	78.1±7.5	70.8±14.5

tailed Wilcoxon two-sample rank sum test (Brown and Hollander 1977). The critical level for each of the ten tests was set at 0.005 to protect against an increased family error rate for the multiple tests. Using Student's *t*-test ($P < 0.01$), differences between gill raker and branchiostegal ray counts from Lake Superior and the Skeena River, B.C. specimens were tested for significance. In addition, meristic and morphometric measurements (with the exception of ray and scale counts) were compared to Siberian data.

Results

The Wilcoxon two-sample rank tests indicated that there was a significant sexual difference in lateral line scales, snout length, head length, maxillary bone length, lower jaw length, body depth, dorsal fin height, anal fin length, anal fin height, and caudal fin length characters. These characters and the range for both sexes are shown in Table 1. All the characters listed indicate that male fish had a significantly larger structure or count with the exception of the anal fin length and height. The anal fin was decisively longer and higher in the female. The remaining characteristics were not significantly different. The male's anterior head region, although significantly larger than that of the female, is composed of structures that are not significantly larger, despite the occasional occurrence of larger degrees of variation in male meristic ranges.

There were also no significant sexual differences in scale characters. All the scales that I examined had a total range of 20–31 circuli, regardless of body length (TL). Where annuli were present, only one was visible. There was no significant correlation between scale circuli counts and total length.

A comparison of Lake Superior data with other similar studies in the Pacific Northwest Coast is presented in Table 2. My work in Marquette County and that of Kwain and Chappel (1978) concern odd and even-year spawning runs, respectively. The odd-year Lake Superior spawning run sampled in 1975 was composed of smaller fish having fewer lateral line scales and gill rakers than was found in the nine spent females collected in 1976 (Kwain and Chappel 1978). There is a strong degree of correspondence between odd-year Lake Superior lateral line scales and other characteristics to data from Canada (McPhail and Lindsey 1970; Scott and Crossman 1973; Hart 1973). There is also a degree of similarity between the even-year Lake Superior lateral line scale counts and those listed by Schultz (1936) for U.S. waters. As one would expect there was no significant differences (Students' *t*-test) between Lake Superior and Skeena River specimens with regard to gill raker and branchiostegal rays.

Morphological studies from six of the Siberian populations indicate that there is little visible difference between Lake Superior population meristic values and the majority of similar values from Siberia (Table 3). Eniutina (1954) studied female characteristics for specimens of 450–460 mm FL of the Amur and Okhotsk populations. The restriction in fork length was made on the basis that female fish show the least amount of variation and are the best representation of the population for most of the life cycle. I compared female characteristics from Marquette County collections (352–420 mm FL) to Eniutina's data in Table 4. The main differences appear to be in head length, body size, lateral line scales, head height, lower jaw length, dorsal fin rays, postdorsal distance, and anal, pectoral, and caudal fin measurements.

TABLE 2. Comparison of the ranges of morphological characteristics for both sexes of adult pink Salmon in tributaries of Lake Superior in Marquette County and Ontario, Canada and in the Pacific Northwest Coast in U.S. and Canadian waters.

	Lake Superior		Pacific Northwest Coast			
Characters	Marquette Co. tributaries	Steel R., Ontario (Kwain and Chappel 1978)	U.S.A. (Schultz 1936)	Canada (McPhail and Lindsey 1970)	Canada (Scott and Crossman 1973)	Canada (Hart 1973)
Fork length	336.2–380.2	410–440			431.8–482.6	
Lateral line scales	148–184	179–218	170–231	147–198	147–205	150–205
Gill rakers	24–31	27–30	27–35	28–32	24–35	26–34
Branchiostegal rays	11–14	10–11		10–15	9–15	10–15
Dorsal fin rays	11–14			10–16	10–15	10–15
Anal fin rays	13–16		14–16	13–19	13–19	13–17

TABLE 3. A comparison of meristic and morphometric characteristics (mean ± SD) for both sexes of pink salmon samples in tributaries of Lake Superior in Marquette County and in Siberia (Dvinin 1952).

Meristic characters	Marquette Co. tributaries	W. Sakhalin population	E. Sakhalin population	Amur population	W. Kamchatka population
(mean counts)					
Total length	389.0±25.8	557.5±2.4	496.2±2.4	426.5±4.7	473.1±3.6
Fork length	358.2±22.0	538.6±2.6	480.2±2.5	395.5±4.2	451.9±3.7
Standard length	324.4±20.4	300.5±2.4[a]	454.7±2.6	410.0±4.3	426.4±3.5
Lateral line scales	163.0±14.3	175.64±0.53	172.9±0.25	170.0±0.07	174.05±1.26
Br. dorsal fin rays	12.2±1.0	10.67±0.06	10.39±0.15	10.75±0.1	10.62±0.6
Br. anal fin rays	14.8±1.1	14.7±0.07	14.02±0.08	14.37±0.11	13.85±0.07
Branchiostegal rays	12.6±0.9	12.18±0.07	12.12±0.08	11.35±0.11	11.87±0.06
First arch gill rays	27.4±3.2	30.03±0.13	19.93±0.15[a]	29.18±0.18	29.27±0.15
(mean counts/mean standard length expressed as a percent)					
Snout length	7.5±1.3	6.41±0.73	4.95±0.09	6.00±0.12	6.36±0.10
Eye horizontal diameter	3.3±0.2	3.62±0.18	3.58±0.06	3.15±0.05	23.07±0.02[a]
Width between eyes	9.6±0.2				
Head length	25.2±7.0	21.79±0.12	22.20±0.09	21.26±0.15	21.71±0.14
Head height	18.5±2.1				
Head length behind eyes	14.7±1.3	12.69±0.07		12.49±0.08	12.71±0.06
Forehead maximum width	29.4±4.3				
Maxillary length	9.6±1.8	8.31±0.06	8.57±0.10	8.65±0.16	8.46±0.09
Lower jaw length	16.6±2.4	14.22±0.12	14.45±0.09	13.38±0.13	13.27±0.12
Lower jaw width	7.8±1.3				
Body depth	27.1±3.9	24.87±0.13	24.78±0.16	23.65±0.25	23.30±0.16
Body thickness	11.5±1.5	11.70±0.07		10.60±0.11	9.74±0.07
Least body thickness	4.4±0.8				
Predorsal distance	49.0±4.1	45.74±0.13		46.24±0.14	45.62±0.14
Postdorsal distance	61.1±3.7	38.25±0.14		40.05±0.15	39.40±0.14
Caudal peduncle length	17.1±2.2	17.16±0.09	17.18±0.18	17.18±0.18	17.45±0.09
Dorsal fin length	12.9±1.5	11.41±0.07	12.28±0.11	11.55±0.13	10.32±0.08
Dorsal fin height	12.7±1.5	11.10±0.07	10.52±0.11	11.00±0.14	10.96±0.09
Ventral fin length	11.4±1.1	14.72±0.08	12.30±0.10	10.86±0.09	11.66±0.07
Anal fin length	15.3±1.7	11.97±0.07	11.55±0.13	11.38±0.08	11.41±0.09
Anal fin height	11.3±1.7	9.62±0.08	8.81±0.09	9.93±0.09	9.18±0.12
Caudal fin length	8.5±2.1	5.69±0.03	5.65±0.08	5.50±0.00	5.90±0.07
Pectoral fin length	15.6±1.3	12.18±0.09	14.12±0.10	14.26±0.11	14.46±0.08
(mean counts/head mean length expressed as a percent)					
Snout length	29.8±5.2	30.01±0.26		27.17±0.32	28.79±0.29
Eye horizontal diameter	13.3±0.8	17.30±0.11		14.93±0.21	14.47±0.14
Head length behind eyes	58.2±5.2	57.59±0.22		58.09±0.30	58.20±0.21
Maxillary length	38.0±7.2	39.22±0.21		40.14±0.35	38.34±0.25
Lower jaw length	65.9±9.4	64.67±0.25		62.72±0.39	60.91±0.24
Forehead width	36.1±5.2	37.09±0.16		33.08±0.12	33.12±0.12

[a]Probably erroneous values.

Discussion

Davidson (1935) noted that dimorphism for secondary sexual characteristics are more pronounced in Pacific pink salmon than in any of the other five *Oncorhynchus* species. The greatest differences were found in the male head and upper predorsal region. A similar pattern of differentiation occurs in the Lake Superior population. Snout length, head length, maxillary bone length, lower jaw length, and body depth are significantly larger in males. The majority of all the remaining characters were not significantly different except that female fish had longer and higher anal fins while males had higher dorsal fins and longer caudal fins. There has been no reported sexual differences in the morphometry of these characters from Pacific populations. These characteristics, therefore, readily identify the Lake Superior population.

It appears that the secondary sex characters of male pink salmon begin to differentiate at about 35–45 d before the end of the life cycle (Davidson 1935). Davidson recorded increases of 19% in the size of the hump, 5% in the head length, 67% in the distance between the tip of the snout to the nares, 3% in the width of the head, 12% in the width between the eyes, and 34% in the distance between the external nares when compared with that of immature males. Externally

TABLE 4. Comparison of female pink salmon meristic and morphometric characteristics (mean ± SD) sampled in tributaries of Lake Superior with Siberian silverly fish of 450–460 mm FL; values for the branched dorsal and anal fin rays from the Amgun R. and Iski R. were given in Eniutina (1954), but not in Ricker (1962).

Meristic characters	Marquette Co. tributaries	Amgun R. (Amur population)	Iski R. (Okhotsk population)	My R. (Maritime Province) population
(mean counts)				
Lateral line scales	155.0±7.2	175.30±1.16	180.60±1.47	
First arch gill rays	27.3±3.2	29.92±0.18	29.80±0.27	
Br. dorsal fin rays	12.0±0.7	11.34±0.09	11.40±0.11	
Br. anal fin rays	14.7±0.9	14.74±0.17	15.04±0.11	
(mean counts/mean fork length expressed as a percent)				
Snout length	6.5±0.7	6.34±0.05	7.20±0.08	5.97±0.05
Head length behind eyes	14.4±0.9	14.15±0.06	14.46±0.09	
Head length	23.7±1.6	20.99±0.06	21.60±0.10	
Head height	18.2±1.4	10.78±0.09	10.76±0.16	
Maxillary length	9.0±1.0	7.86±0.04	8.60±0.11	7.84±0.09
Lower jaw length	14.6±0.7	12.18±0.06	13.60±0.12	12.46±0.11
Body depth	24.8±2.2	24.47±0.13	22.80±0.21	23.58±0.19
Predorsal distance	47.4±2.2	45.52±0.13	46.36±0.15	44.50±0.28
Postdorsal distance	60.2±7.0	40.96±0.37	39.72±0.26	
Caudal peduncle length	16.9±1.4	18.01±0.18	17.24±0.12	
Dorsal fin length	12.1±0.9	10.62±0.08	10.48±0.12	9.91±0.09
Anal fin length	15.6±1.9	11.59±0.15	12.20±0.12	9.95±0.33
Anal fin height	12.9±1.1	10.63±0.08	11.36±0.13	
Caudal fin length	22.1±4.6	15.42±0.22	14.74±0.12	

the sexes are identical when immature in the Pacific Ocean and presumably the same is true in Lake Superior. There have not been any collections recorded for immature pink salmon from Lake Superior. However, the freshwater population demonstrates the same pattern of head and hump differentiation in males as in the Pacific stocks.

Davidson (1935) did not compare morphometric measurements between odd and even-year spawning runs. Besides a greater abundance, odd-year adults are usually larger and heavier than those sampled in even-year periods in British Columbia (Godfrey 1959). However, the Marquette County 1975 collections were composed of fish that were obviously smaller than those taken in the first even-year collection made in 1976 from Ontario (Kwain and Chappel 1978). This may be the result of genetic differences between stocks, although Kwain and Chappel questioned the existence of two groups in Lake Superior. Instead, they suggest that the even-year spawning group may have originated from 3-yr-old odd-year fish. It appears that the Lake Superior population has both smaller sized odd-year spawning fish and larger even-year spawning fish.

In comparing similar characteristics between Lake Superior, U.S. Pacific, and British Columbia populations, the Lake Superior population is smaller at maturity and has a lower range of gill rakers than Schultz (1936) recorded, but is similar to a range listed by Scott and Crossman (1973) for Canada. Pritchard (1945) found that mean gill raker counts were useful for determining significant differences between pink salmon in various rivers in British Columbia. However, Amos et al. (1963) suggested that there was little variability for such characters within their area of study. The latter authors found that by using discriminant analysis, total vertebrate, scale intermediate zone length, and dorsal fin ray characters permitted correct separation of 98% of the specimens between American and Asian morphotypes. Pearson (1964) was able to use scale characters, branchiostegal rays, and vertebrate characteristics to distinguish between American and Asian groups. Gill raker counts from the odd-year Lake Superior collection are within the Canadian Pacific Coast data limits but not those of the U.S.A. (Table 2) which may have been drawn from even-year fish. There is some similarity between the even-year Steel River count and that of Schultz (1936). Dorsal fin ray counts also agree with Canadian results. In considering the lateral line scale, gill raker, branchiostegal ray, dorsal fin ray, and anal fin ray counts as well as the *t*-test results between Marquette County and the Skeena River, it is quite obvious that the Lake Superior population strongly resembles the British Columbia population from which they originated. However, there is no record of such a great degree of male sexual differentiation or larger fin characteristics from anywhere in the Pacific.

It is apparent from Tables 3 and 4 that Lake Superior

and Siberian population characteristics often differ from each other. Body lengths, lateral line scales, dorsal fin rays, snout length, head length, head length behind eyes, maxillary length, lower jaw length, body depth, predorsal distance, postdorsal distance, dorsal fin length and height, anal fin length and height, caudal fin length, and pectoral fin length all appear to be substantially different.

The eight Pacific populations of pink salmon each have distinctive features. The West Kamchatka is noted for a thin caudal peduncle, the Okhotsk has a long snout and a long anal fin, the Amur has a deep caudal peduncle and long pectoral fin, the Maritime Province has a short tail, short anal insertion, short lower jaw, and a short and narrow maxillary, the West Sakhalin has a long ventral fin, short pectoral fin, and long lower jaw (Ricker 1962). Dvinin (1957) added that the West Sakhalin population had longer pelvic fins than found in the East Sakhalin. Ricker (1962) stated that the Maritime Province population, or the Primor'e (Eniutina 1954), has the most distinctive appearance of all pink salmon stocks, although Dvinin (1957) described the Amur stock as a separate taxon. The distinctive characters for the Lake Superior population are associated with shorter body length, larger and longer fins, and a greater degree of differentiation in the male head and hump.

This study shows that the Lake Superior freshwater population demonstrates sexual differentiation that exceeds the degree reached by the Soviet populations and probably that of the U.S. and Canadian Pacific populations as well. It may be that the slower rate of growth of pink salmon in Lake Superior (Kwain and Chappel 1978) causes an exaggeration in the size of the fins and male sexual characteristics in the head, although the length measurement itself is unlikely to be a factor when considering such variations (Pearson 1964). The 1955 broodyear stock fingerlings that successfully reproduced were probably so isolated and/or so few in numbers that genetic drift may have allowed the unique and distinctive characteristics of the Lake Superior population to emerge.

Acknowledgments

I extend my appreciation to the Marquette Fisheries Research Station, Michigan DNR for allowing me to use the 1975 Little Garlic River collection in this study, as well as to Mr Murray H. Amos, Northwest and Alaska Fisheries Center, Mr H. T. Bilton, Nanaimo Pacific Biological Station, and Mr Ron Kadowaki, Fisheries-Pacific Region, for allowing me to use source data from Skeena River pink salmon. I am also thankful for being allowed to use the facilities at Northern Michigan University for this project. Ms Diane Stevenson gave useful advice concerning the statistics used here; Mr Steve Yeo and Mr Robert Henderson reviewed the manuscript.

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NOTES

Laboratory Study of Cylindrical Sedimentation Traps

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LAU, Y. L. 1979. Laboratory study of cylindrical sedimentation traps. J. Fish. Res. Board Can. 36: 1288–1291.

Observations of the motion of fluid particles in cylindrical sedimentation traps showed that with an increase of the aspect ratio, there is also an increase in the Reynolds number below which neutrally buoyant droplets that were placed near the floor of the trap would remain in the bottom layer. The dependence of the fluid motion on these two dimensionless variables was demonstrated using traps of different diameters. For single cylindrical traps, the experimental results can be used to obtain estimates of the Reynolds number below which resuspension of settled material would not be expected to occur.

Key words: sedimentation trap, aspect ratio, Reynolds number, limnological instrument

LAU, Y. L. 1979. Laboratory study of cylindrical sedimentation traps. J. Fish. Res. Board Can. 36: 1288–1291.

Des observations sur le mouvement de particules fluides dans une trappe de sédimentation cylindrique démontrent qu'à mesure qu'augmente le rapport d'exposition, il y a augmentation du nombre de Reynolds au-dessous duquel des gouttelettes à flottabilité neutre placées près du plancher de la trappe demeurent dans la couche du fond. Nous démontrons la dépendance du mouvement d'un fluide de ces deux variables sans dimension, nous servant de trappes de diamètres différents. Dans le cas de trappes cylindriques uniques, les résultats expérimentaux peuvent servir à estimer le nombre Reynolds au-dessous duquel on ne peut s'attendre à la resuspension de matériel déposé.

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SEDIMENT traps are used by many environmental scientists to measure the settling rate of low density organic particles in lakes and oceans (Anderson 1977; Soutar et al. 1977). These particles have very small settling velocities, varying between 10^{-5} and 10^{-2} $cm \cdot s^{-1}$ (McCave 1975) and the downward settling flux of these particles through the water column is very small. Many different designs of sediment traps exist and their efficiency in trapping particles vary with design as well as with turbulence in the water body (Hargrave and Burns 1979). The hydrodynamic characteristics of the traps have seldom been considered.

Hargrave and Burns (1979) discussed the design of sediment traps and identified three major considerations. First, the exchange of water between the trap and the surrounding water can lead to errors if the cross-sectional area of the trap differs from the area of the mouth of the trap. Second, the settled material may be resuspended or scoured out of the trap, causing a decrease in the catch for the trap. Third, the flow over the mouth of the trap may be deflected upward, resulting in a decrease in the amount of material entering the trap. They suggested that, in order to eliminate the first problem, the basic shape of a trap should be a cylinder open at the top, thus maintaining equal concentration of particles inside and outside of the trap.

The second problem, that of resuspension of settled material, depends on flow conditions as well as trap dimensions. Therefore, I investigated the fluid motions inside cylindrical traps to obtain some guidelines for their use. In particular my objective was to show that fluid motion near the bottom of a trap increases with increasing Reynolds number and decreasing aspect ratio of the trap and that the aspect ratio required to prevent resuspension of settled material is a function of Reynolds number.

Experimental method — Sediment traps were constructed from acrylic tubing of various diameters and lengths, with bases glued to the bottom ends. Three sizes of tubing were used, with diameters of 3.4, 5.0, and 8.8 cm. The heights of the traps varied from 21.2 to 50.0 cm.

Tests were conducted in the 2-m wide flume in the Hydraulics Laboratory, National Water Research Institute. Water depth was kept constant at approximately 70 cm. Flow velocity was measured using an Ott current meter

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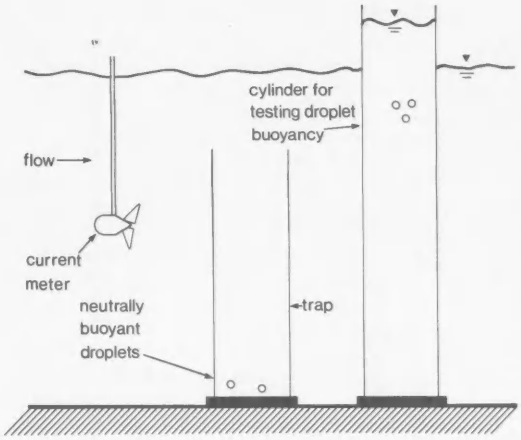

FIG. 1. Experimental set-up for the observation of droplet motion.

placed about 15 cm below the water surface. Velocities ranged from about 3 cm/s to 75 cm/s.

Neutrally buoyant oil droplets were used for observation of the motions in the traps. The droplets, about 3 mm in diameter, acted essentially as distinct fluid particles and enabled fluid motions near the bottom of the traps to be detected. With steady flow conditions in the flume, four or five droplets would be dispensed into the trap using a long needle and syringe. The droplets were placed as close to the floor of the trap as possible, usually within 1–2 cm. Observations were made through the glass windows of the flume to determine whether the oil droplets stayed in the bottom layer where they were placed or moved upwards through the trap. If all of the droplets still remained at the bottom after about 10 min, the flow velocity in the flume was changed and the test was repeated. Figure 1 illustrates the test set-up.

The oil used was Meriam oil which is normally used as manometer fluid. Oils of different densities were mixed to a specific gravity of about 1.0. Prior to a test, several droplets were dispensed into a cylinder of water which sat in the flume downstream of the trap. The top of the cylinder was out of the water surface in the flume and therefore the water inside the cylinder was always still but was at the same temperature as the flume water. By observing the droplets in the cylinder, it could be decided if adjustments were required to make the oil mixture neutrally buoyant. When a proper mixture was obtained, the droplets would remain motionless in the cylinder. This mixture was then used in the trap. The oil was red and could be readily observed.

In most of the tests, droplets were also placed in various different locations in the traps and the motion of these droplets was observed. A few tests were also made using traps with cylindrical baffle tubes inserted.

Results and discussion — In all the tests, droplets which were placed in the top two-thirds of the traps all escaped from the traps within a very short time. A droplet would, in general, meander its way up the trap and, near the top, be swept up in an eddy and carried out of the trap. Occasionally, a droplet would swirl about several times in the separation region just above the trap before being carried downstream. Within one or two diameters from the top of the trap, the droplets circulated with velocities comparable to the ambient flow velocities. The speed at which droplets escaped depended on the flow velocity as well as the ratio of trap height to trap diameter (aspect ratio). At any given aspect ratio, the motion of the droplets increased with velocity. As the aspect ratio increased, the amount of motion at the same relative position in the trap decreased. The movement of droplets out of the bottom layer usually occurred wihin the first few minutes. Very little change was generally observed after the first 5 min.

The flow induced in a cylindrical trap by the ambient current can be expected to be governed by the ambient velocity μ, the kinematic viscosity of the water ν, the height of the trap h and the diameter of the trap d. Except for very small diameters which have little practical significance, the wall roughness should not be an important factor. It is also assumed that the wall thickness of a trap is small compared with its diameter and can be neglected. Using dimensional analysis with the above four parameters, it can be shown that motion in the traps is governed by two dimensionless variables, namely, the aspect ratio h/d and the Reynolds number $\mu d/\nu$.

Results of over 100 tests are given in Fig. 2. The data points are designated as 'stay' when all the droplets in the bottom layer remained or 'escape' when all the droplets moved out. Occasionally, one of the droplets would move out but the rest remained. This condition was designated as 'borderline.' Because these were all based on visual observations, they were sometimes subjective. Figure 2 shows that, at a low aspect ratio of about 5.0, escape started at a Reynolds number of about 7000, whereas when the aspect ratio was increased to 10.0, it started at Reynolds number of about 20 000. For the same diameter traps, this means that the velocity at which particles near the bottom begin to move up the trap has increased 2.8 times. For each trap, the data points progressed from 'stay' to 'borderline' to 'escape' as the velocity increased. Occasionally, there were some inconsistencies and the demarcation between each region was not distinct. This is to be expected because of the subjectivity involved, compounded by the motions which are sometimes inadvertently set up by the dispensing needle and the difficulty in deciding whether a droplet was initially in the bottom layer.

Figure 2 shows that escape of the droplets was governed by the aspect ratio and the Reynolds number and not by the size of the trap because there are no appreciable differences between the results for the three different diameters. However, this does not mean that the trap diameter is not significant. If two traps have the same aspect ratio but one has twice the diameter of the other, the Reynolds number $\mu d/\nu$, at which 'escape' starts will be the same for both traps, but the velocity at

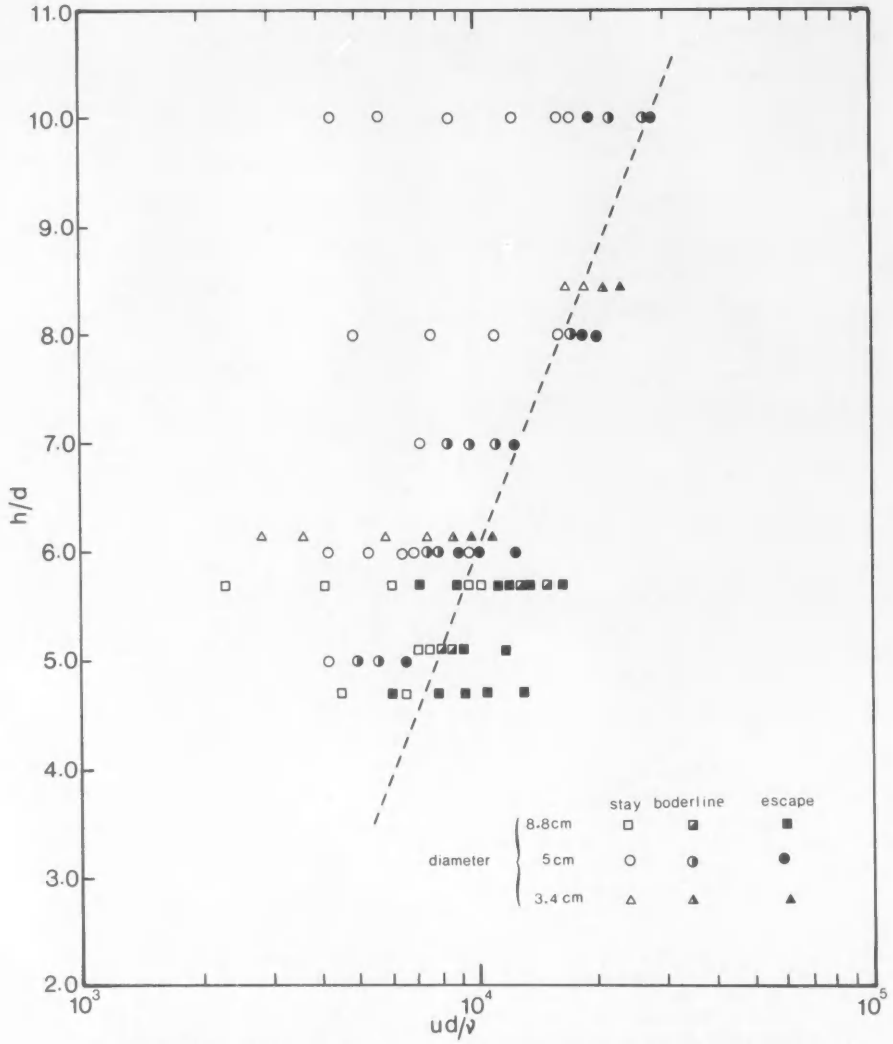

FIG. 2. Dependence of droplet motion on aspect ratio and Reynolds number. The dashed line indicates approximately the separation between the 'stay' and 'escape' regions.

which particles start to move out of the bottom layer will be twice as high for the smaller trap as that for the larger trap.

If the trap aspect ratio and Reynolds number fall on the left of the line in Fig. 2, then the fluid particles near the floor of the trap can be expected to stay in the bottom layer. For example, for a 10-cm diameter trap 70 cm in height, the Reynolds number is given as about 1.25×10^4. Therefore, below a velocity of about 13.7 cm/s, there should be no movement of particles out of the bottom of the trap.

Because of the cohesion which exists between settled particles, the shear stresses which will be required to put the particles into resuspension in the natural situation can be expected to be larger than those required to move fluid particles out of the bottom layer. If conditions are such that fluid particles do not move out of the bottom layer, it should be safe to assume that particles which have settled in the trap would remain in the trap. Therefore, the dashed line in Fig. 2 can be considered as a conservative estimate of the aspect ratio required at a given Reynolds number to prevent loss of settled particles by resuspension.

Gardner (1977) investigated the performance of traps of different design in a recirculating flume filled with seawater containing suspended sediments. He obtained

the efficiency of each trap by comparing the amount of settled material per unit area for the trap with that for the flume floor. The cylindrical traps which Gardner used has aspect ratio equal to 1.0 and 2.3. No noticeable influence of aspect ratio on trapping efficiency was found. However, the flow velocities were mostly below 5 cm/s with a maximum of 9.5 cm/s and the Reynolds numbers were approximately equal to 3×10^3. It can be seen from Fig. 2 that, at such low Reynolds numbers, settled material can be expected to stay in the traps. Gardner also deployed cylindrical traps in a number of field stations and compared their collection rates. In these experiments, maximum velocities reached 15 cm/s or higher. It was found that the amount of material collected increased as the aspect ratio of the traps increased. At locations where flow velocities were higher, the increase in collection rate with aspect ratio was more rapid. Even though Gardner did not specifically investigate the problem of resuspension which also is not the only factor affecting the collection rate, his results are entirely consistent with the present findings.

A few brief observations were made using traps with cylindrical baffle tubes which were grouped together to completely fill the trap. It was evident that, to be effective, the baffle tubes must go right to the bottom of the trap. With baffles which went part way into the trap, droplets which were placed below the baffles and near the bottom of the trap were moved out just as quickly as when there were no baffles.

Observations were then made using a 10-cm diameter trap, 12.3 cm high that was packed with 2.2-cm diameter baffle tubes. The baffle tubes were sealed at the bottom and were of the same height as the trap. This trap was compared with a single 2.2-cm diameter tube placed in the flume at the same time. Because of the small diameter of the baffles, the oil droplets could not be used for observation because they stuck easily to the walls of the tubes. Instead, observations were made on a colored layer which was formed on the bottom of the tubes by dropping in crystals of dye. Because the baffles were all sealed at the bottom, they were essentially a group of 2.2-cm diameter traps bunched together. However, motion of the dyed interface was observed in the middle tubes considerably before it was detected in the tubes at the front or the rear of the bundle or in the single 2.2-cm trap. At a velocity of about 60 cm/s, dyed streaks started to rise from the tubes at the center. It was not until the velocity reached about 70 cm/s that similar activity was observed in the single trap. It appeared that the baffle tubes in the front and the rear of a trap act more like a single trap but that motion occurs in the center baffle tubes at a lower velocity.

Acknowledgments — The author expresses his appreciation to N. M. Burns who suggested the problem and provided many helpful discussions. F. M. Boyce offered helpful comments on the manuscript. The assistance of J. Heidt in conducting the experiments is also gratefully acknowledged.

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OBITUARY/NÉCROLOGIE

Russell Earle Foerster

1899-1978

Earle Foerster was born in Neepawa, Manitoba, on May 29, 1899. He came to Vancouver in 1917 and entered the newly-organized University of British Columbia. After obtaining his Bachelor of Arts in Biology in 1921, he spent a summer at the Pacific Biological Station. The director, Dr C. McLean Fraser, suggested he identify the local Hydromedusae, and this provided material for an M.A. degree. In 1923 he turned to a study of sockeye salmon, which developed into a lifelong interest and occupation. During the next few years field work alternated with advanced study at the University of Toronto, which awarded him the Ph.D. degree in 1925. In 1930, at the unusually early age of 31, he became a Fellow of the Royal Society of Canada.

During the 1920s great disappointment prevailed because of the apparent inadequacy of the Pacific salmon hatcheries, and particularly their failure to restore the Fraser River sockeye runs to anything like their early level of yield. In 1925 the Biological Board of Canada was asked to evaluate the various aspects of the hatchery program and was given funds for this purpose. A small laboratory was built at Cultus Lake, with Dr Foerster in charge. In collaboration with the Hatchery Service an experiment was set up to compare natural propagation of sockeye with two currently used artificial procedures: eyed-egg plantings and fry liberations. This was to include 4 replications of each method over a period of 14 years, during which both adult fish and the smolts they produced were counted into and out of the lake. The experiment attracted wide attention almost immediately, and stimulated similar studies in places as distant as Kodiak Island and Kamchatka. The upshot was that for small runs the hatchery procedures produced about twice as many smolts as natural propagation; but this was far from being an economic return at the low fish prices then prevailing, and the hatchery contribution to the total Fraser catch was insignificant.

Among the other studies conducted by Foerster were comparisons of different egg-taking techniques, the value of pond rearing of young sockeye for different lengths of time before release into the lake, production of hybrids among the 5 species of Pacific salmon, an attempt to turn young of freshwater kokanee into anadromous sockeye, and an evaluation of predator control as a means of increasing smolt production, and of the efficacy of using nonnative stocks in attempting to restore lost runs of sockeye above the canyons of the Fraser River.

In 1932 Dr Foerster moved to Nanaimo when he was appointed Assistant Director of the Pacific Biological Station, but he continued in charge of the sockeye investigations. When the International Pacific Salmon Fisheries Commission was organized in 1937, Earle became its chief scientist. He led the field parties that tagged sockeye in the Fraser canyon, and identified the river levels that presented difficulty to the passage of salmon at Hell's Gate.

In 1940, however, Earle returned to the Fisheries Research Board as Director of the Nanaimo Station. He held this position throughout the difficult war years and into the start of the postwar expansion. The latter included an ambitious survey and evaluation of salmon production in the Skeena River system and elsewhere, and expanded studies of herring and groundfishes. In addition, his energy and persistence were largely responsible for the erection of a badly needed new building for the Station, at a time when funds and materials were still very tight.

By 1950 Dr Foerster felt that he had "served his term" as administrator, and went back to research work until he retired in 1962. During this period he learned to read Russian, in order to become familiar with the large volume of salmon investigations on the west side of the Pacific. Eventually he put together a 420-page book "The Sockeye Salmon," which won the United

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States Wildlife Society's award for best fishery publication of the year. He also contributed to the deliberations and the documentation of the International North Pacific Fisheries Commission.

Earle Foerster was always keenly interested in the communities where he lived and gave generously of his time to local enterprises. These included the Chilliwack Kinsmen Club, and in Nanaimo the Rotarians, the Symphony Society, and the Salvation Army. He also served a term on the Senate of the University of British Columbia.

Earle's death occurred on September 17, 1978. He is survived by his sons Darryl, Ronald, and Douglas, his wife Gwendolyn having died on May 3, 1979.

W. E. RICKER

BOOK REVIEWS/COMPTES RENDUS

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Effects of Pollutants on Aquatic Organisms. *Edited by A. P. M. Lockwood. Cambridge University Press, London, New York, and Melbourne. 1976. x + 193 p. $7.50. $22.50 ($8.95 paper).*

The purpose of this volume is to provide a wide variety of experimental approaches to pollution and thereby serve as an introduction for undergraduates and research students to a rapidly expanding field, aquatic toxicology. These approaches are preceded by Gwyneth Howell's Introduction which gives a rational and thorough scheme of pollution investigation and assessment, starting with the recognition of existing environmental or biological damage. While it does not specifically address toxicity testing as a screening approach to prevent pollution, the Introduction does provide a concise presentation of fundamental concepts, such as relating chemical concentrations in the field to actual harmful effects on biota; emphasizing the importance of obtaining dose–response relationships; considering the effects of fluctuations in chemical concentration and speciation; relating responses in individuals to populations, and, ultimately, to communities; establishing a priority listing of chemicals in order to direct scientific effort, and finally, the most important area of "developing a fruitful interaction between laboratory and field investigations."

With a couple of exceptions, the remaining eight chapters present a thorough review of general topic areas with the author's research given the perspective of specific examples of work within a given area. These areas include: a clinical toxicological approach, measuring some hematological and biochemical sublethal effects of cadmium in the flounder; effects of low dissolved oxygen, high carbon dioxide, ammonia, and phenol on urinary cumulative production and flow rate, as well as on electrolyte concentration changes in serum, urine, and water surrounding the head region of rainbow trout; various aspects, such as concentrations in salt water, plankton, and eight species of marine fish, toxicity, uptake, distribution, metabolism, release, tainting, and sublethal behavioral effects, of petroleum hydrocarbons in marine zooplankton and fish with emphasis on differences in composition of crude oils and petroleum products; effects of petroleum hydrocarbons on general physiological processes in unicellular algae with emphasis on algal photosynthetic machinery and ATP production; the Controlled Ecosystem Pollution Experiment (CEPEX) approach of extending laboratory measurements of lethal and sublethal responses to copper and mercury by marine zooplankton to the field by enclosing a portion of the aquatic ecosystem, using transparent, flexible, plastic containers; and, the effects of wood pulp fiber, low dissolved oxygen, cadmium, chromium, nickel, and zinc on fish cardiovascular and respiratory systems.

Two chapters, one on heavy metal tolerance (by G. W. Bryan), and the other on distribution, transport, and physiological significance of organochlorine compounds (by R. F. Addison), were especially well written, and gave indepth and broad treatment to the subjects. Bryan addresses tolerance development after a thorough discussion of essential, related processes, such as absorption from solution and from food or particles, excretion and regulation, and transformation and storage. The 110 references cited in this chapter reflect that a multitude of salt and freshwater species ranging from algae to marine mammals were considered, and that accumulation and toxicological responses by aquatic organisms to 17 metals were presented. Because of the relative wealth of available information (76 references cited), Addison chose to write on three categories of chlorinated hydrocarbons: the DDT group of insecticides, the polychlorinated biphenyls, and the cyclodiene insecticides, emphasizing the effects of aquatic organisms on these chemicals. The introduction on historical development, uses and physical properties of these chemicals, is followed by a concise, yet thorough, presentation on mechanisms of uptake, distribution, and elimination by aquatic organisms. Addison concludes with a brief discussion on the responses of organisms to these chemicals, stating that future reviews should emphasize biochemical and physiological sublethal effects in order to provide meaning to the voluminous amounts of available residue data. In sum, each of these very relevant chapters should continue to provide the research student with excellent reference points.

During the past 4 years there have been several books published that compile the proceedings of a conference or symposium on aquatic toxicology. The majority of those published in North America largely emphasize approaches and needs of the United States. Thirteen of the 21 contributors to this well-indexed volume, however, are from Scandinavian or United Kingdom countries and possibly reflect more concern for detecting existing polluted aquatic environments. Therefore, in addition to providing information on the approaches previously described, this volume should be added to laboratories and libraries to give a more complete appreciation of aquatic environmental toxicological research.

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(R132)

Books received/Livres reçus[1]

May/mai 1979

Fishes of the Delaware Estuaries: a guide to the early life histories. *Johnson C. S. Wang and Ronnie J. Kernahan. EA Communications Div. of Ecological Analysis, Inc., Towson, Md. 1979. xxxi + 410 p. $22.50* (Over 600 illustrations, 750-plus references and keys to 112 species of the area are presented in this spiral-bound manual. Each species has extensive descriptions of early life histories).

*__The Natural History of Native Fishes in the Death Valley System.__ *David L. Solz and Robert J. Naiman. Natural History Museum of Los Angeles County, Los Angeles, Calif. 1978. ix + 76 p. $7.50 + $1.50 postage and handling from publisher.* (This is No. 30 in the Museum's Science Series; it is of particular interest to those concerned with preservation of desert fauna.)

Fisheries of Australia. *Peter Pownall. Fishing News Books Ltd., Farnham, Surrey, England. 1979. x + 149 p. £7.50.* (A concise, basically nontechnical description of the history and present day development of Australian fisheries. There is also some material on Papua New Guinea, Indonesia, and New Zealand fisheries.)

*__Economics of Fisheries.__ *Rögnvaldur Hannesson. Universitatsforlaget, Bergen, Oslo and Tromsø, Norway. (Columbia University Press, Irvington-on-Hudson, NY) 1979. 156 p. $18.00.* (A highly condensed, soft-covered book on economic theory as applied to fisheries; comparisons of several yield models are given.)

The Edible Crab and its Fishery in British Waters. *Eric Edwards. Fishing News Books Ltd., Farnham, Surrey, England. 1979. 142 p. £4.85.* (A concise book on the present status of the crab fishery, including chapters on biology, fishing methods, processing and population dynamics. The present state of the stocks is also discussed.)

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[1]Entries in this list *not* marked by an asterisk are available for review by interested readers for a 3-month period from the time of publication of the list. For information, please write to the Book Review Editor.

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COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

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Freshwater Fishes of Canada

W. B. SCOTT AND E. J. CROSSMAN

For many years there was an acute need for a publication on the identification, distribution, biology, and economic importance of the freshwater fishes of Canada. In 1973, Bulletin 184 of the Fisheries Research Board entitled *Freshwater Fishes of Canada* was published. A French translation entitled *Poissons d'eau douce du Canada* appeared in 1974. A separate Errata sheet providing corrections to the first English edition was circulated in 1975 and those corrections were incorporated in 1975 English and French reprints. The French edition was reprinted without further change in 1978.

The need in 1978 to reprint the English edition provided an opportunity for further improvements. The 1979 reprint of the English Edition is not a revision. It does, however, incorporate corrections not available earlier, and in addition includes a new introductory section. That section provides reference to 11 species new to the fauna, not included in the earlier editions, clarification of problems discovered in earlier printings, and a limited and selected amount of new information on some species.

W. B. Scott is Executive Director of the Huntsman Marine Laboratory, St. Andrews, N.B. He is Research Associate, Department of Ichthyology and Herpetology, Royal Ontario Museum and also Professor, Department of Zoology, University of Toronto.

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